Small-scale spatial patterns of *Austrovenus stutchburyi* in natural and translocated beds

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Abstract

Ecosystems are patterned and patchy as a result of spatial and temporal variation in the abundance and distribution of essential resources, as well as due to geological and ecological processes. Large-scale patterns are usually formed by abiotic stressors while small-scale patterns are a result of biotic factors such as inter- and intra-specific interactions. Many suspension feeding bivalves have been reported to form both small- and large-scale spatial patterns in soft-sediment environments, in a response to boost resilience from environmental stressors and increase facilitation. However, small-scale spatial patterns of infaunal suspension feeding bivalves are currently not as well studied for, despite playing important roles in ecosystem functioning e.g. eutrophication control, resuspend buried nutrients and modify habitats through increased bed roughness. This thesis set out to recognize small-scale spatial patterns of *Austrovenus stutchburyi* and whether patterns differed with density or environmental properties in Tauranga Harbour. A field survey was used to distinguish small-scale spatial patterns of *Austrovenus stutchburyi* in nine established *Austrovenus stutchburyi* beds. At each site a 4 m^2 plot was established in a 'low', 'medium' and 'high' density section of *Austrovenus stutchburyi* aggregates, with core samples taken at 0.5 m intervals within the plots. *Austrovenus stutchburyi* were then transplanted at low, medium and high densities in 4 m^2 plots into an area of low ambient densities to observe any spatial pattern formation and environmental effects with density. *Austrovenus stutchburyi* did not exhibit spatial patterns no different from random in natural beds and was not dependent on density or environmental variables. This was indicated by most of the plots accepting the null hypothesis of Moran's *I* which indicates a random distribution. Following the same sampling design as the field survey a translocation experiment was performed to

distinguish any small-scale spatial patterns of *Austrovenus stutchburyi* in a low ambient density environment. Transplanted *Austrovenus stutchburyi* beds exhibited clustering in high density treatments, indicated by a positive Moran's *I* value in all three high density plots (0.335 – 0.420). Both low and medium plots exhibited random patterns, accepting the null hypothesis of Moran's *I*. Transplanted *Austrovenus stutchburyi* beds significantly improved chlorophyll *a* content with increasing density treatments as chlorophyll *a* increased by almost a factor of two between ambient and high plots from 11.3 µg g^{-1} dw to 20.4 µg g^{-1} dw. However, only a small increase in organic matter content was observed and no modifications were seen towards sediment grain size properties. The results from this study can enrich the knowledge of the currently understudied small-scale patterns of infaunal suspension feeding bivalves including acting as a baseline for future hypotheses and sampling schemes. There is also potential for the high-density translocated plots to act as nursery grounds for reseeded juvenile *Austrovenus stutchburyi* due to the modified environment becoming nutrient-rich further improving conservation and restoration of estuarine habitats.

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Chapter 1

Introduction

1.1 Spatial patterns in ecology

Ecosystems are patterned and patchy (Rietkerk & van de Koppel, 2008) as a result of spatial and temporal variation in the abundance and distribution of essential resources, as well as geological and ecological processes. The range of physical mechanisms of this environmental heterogeneity (e.g. water availability, water flow or sediment dynamics) and patterns formed by habitat-forming organisms are well documented. For example, arable farmland, with regularly managed fields divided by semi-natural field boundaries, contains a mosaic of habitats (Stewart *et al.*, 2000). Arid bush and grasses are also characterized by multiple distinct habitat types due to the formation of stripes, labyrinths, spots and gaps as a direct response to the short-distance positive feedback between vegetation and water availability (Figure 1.1) (Rietkerk & van de Koppel, 2008; von Hardenberg *et al*., 2001). Likewise, divergence of water flow around patches of vegetation within salt marshes increase erodibility, limiting vegetation growth just outside patches at a small-scale and ultimately affecting the landscape formation of this ecosystem (D'Alpaos *et al*., 2007; Temmerman *et al*., 2007). Spatial structure is thus important to research as spatial structure mediates the flow of individuals and resources over space and time (Lindenmayer & Fisher, 2013).

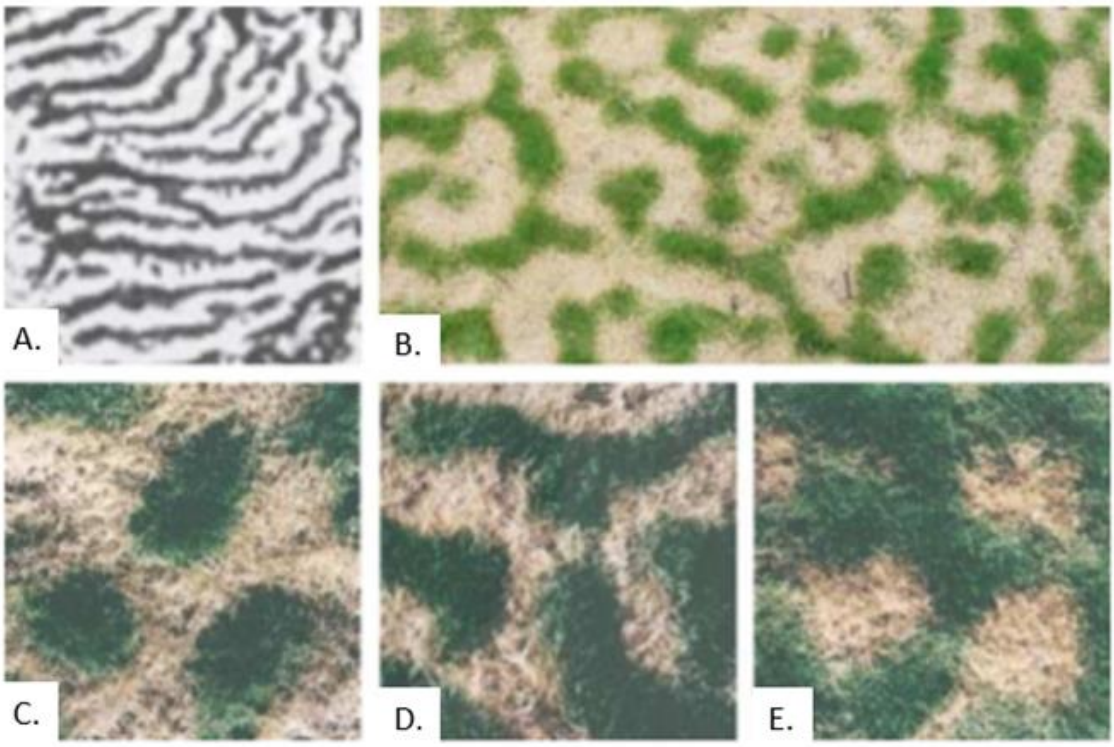

Figure 1.1: Vegetation spatial patterns. Bands (A) of 'tiger bush' on a hillslope in Niger. Labyrinth (B), spots (C), stripes (D), and holes (E) of perennial grass *Paspalum vaginatum* located in northern Negev. The scales in the size of biomass patterns varies from centimetres (B, C, D, E) to tens of metres (A). Original image from von Hardenberg *et al*. (2001).

Ecological processes that categorize and impact landscapes are often spatially structured, and both spatially and temporally scale dependent (Legendre *et al.*, 1997). Spatial characteristics are therefore crucial in conceptualising present-day ecology. The response of organisms to habitat patches varies with scale and a hierarchical model was developed by Kotliar & Wiens (1990) to class patch structure at a variety of scales. Although, scale should not be solely related to the environment but instead a concept affiliated to observation and analysis (Raudsepp-Hearne & Peterson, 2016). Visualization of the concept of scale through the illustration of the nitrogen cycle is depicted in Figure 1.2. The concept of scale has grown rapidly in ecology and has been applied extensively to terrestrial and more recently marine environments (Schneider, 2001).

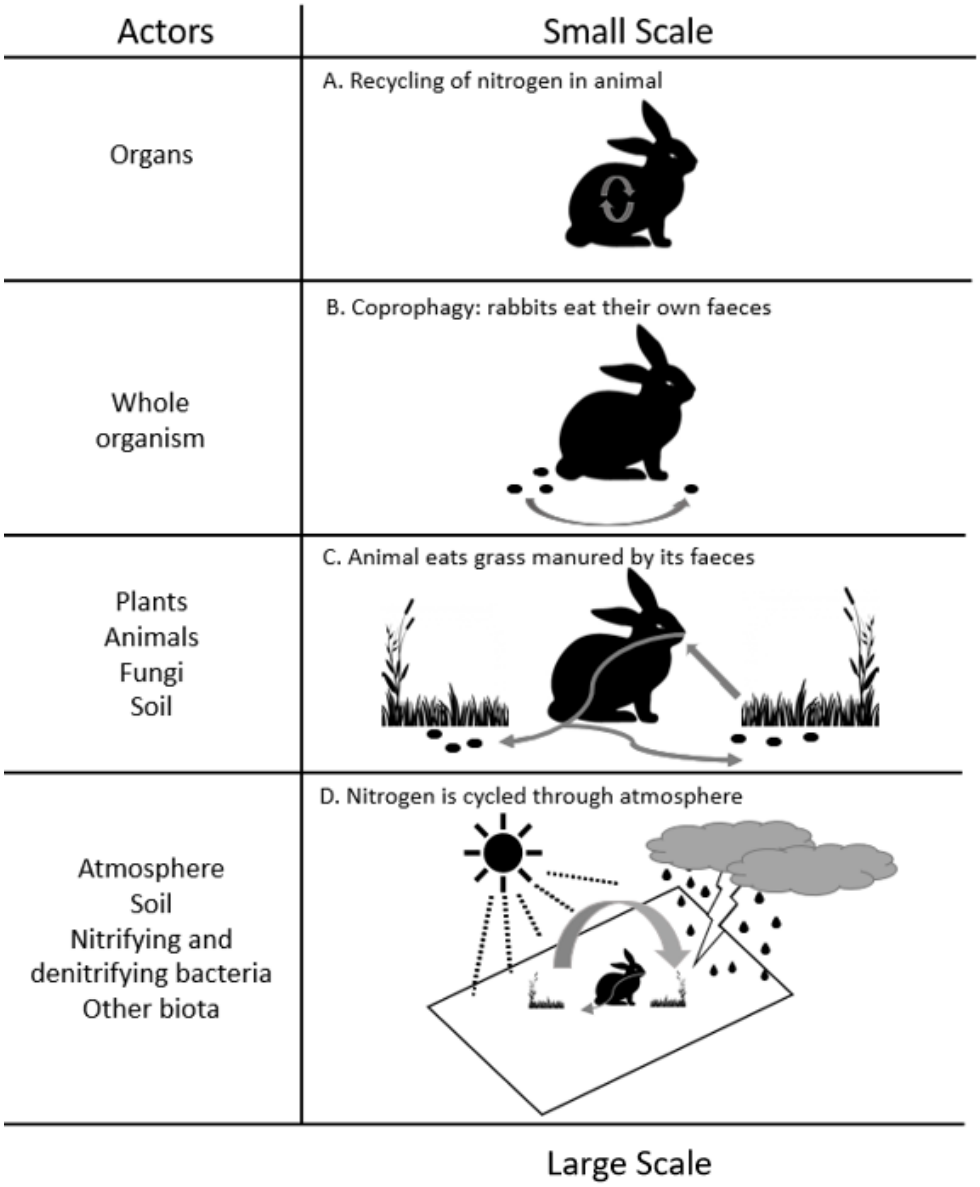

Figure 1.2: The nitrogen cycle process presented at small to large scales. Adapted from Allen & Hoekstra, 1991.

Soft sediment environments are particularly important to research as they are expansive ecosystems, covering 70 % of the ocean seafloor and are commonplace in coastal environments (Snelgrove, 1997). These environments provide many ecosystem services including habitats for a variety of organisms, acting as a barrier from flood and storm events, high primary production, reduce eutrophication risk and have cultural services such as recreational use and cultural heritage (Beaumont et al., 2007; Edgar *et al*., 2000; Piehler & Smyth, 2011). These ecosystems are also easily accessible and have been

extensively researched providing a plethora of supporting ecological knowledge for future work. Intertidal flats can include visibly large patches of epibenthic populations, e.g. seagrass meadows, mussel beds and microphytobenthos (MPB) (Blanchard *et al*., 2000; Coppa *et al*., 2019; De Brouwer *et al*., 2000; van de Koppel *et al*., 2005, 2008) and separating these patches are usually areas of "homogeneous-looking substrate". Although these ecosystems are complex and dynamic, they appear visibly homogeneous since below the sediment, spatial complexity and various phylum of organisms are hidden (Figure 1.3). Invertebrates that live beneath the sediment surface are the dominant assemblages of these flats and are often not as homogeneous as what appears on the surface (Thrush, 1991).

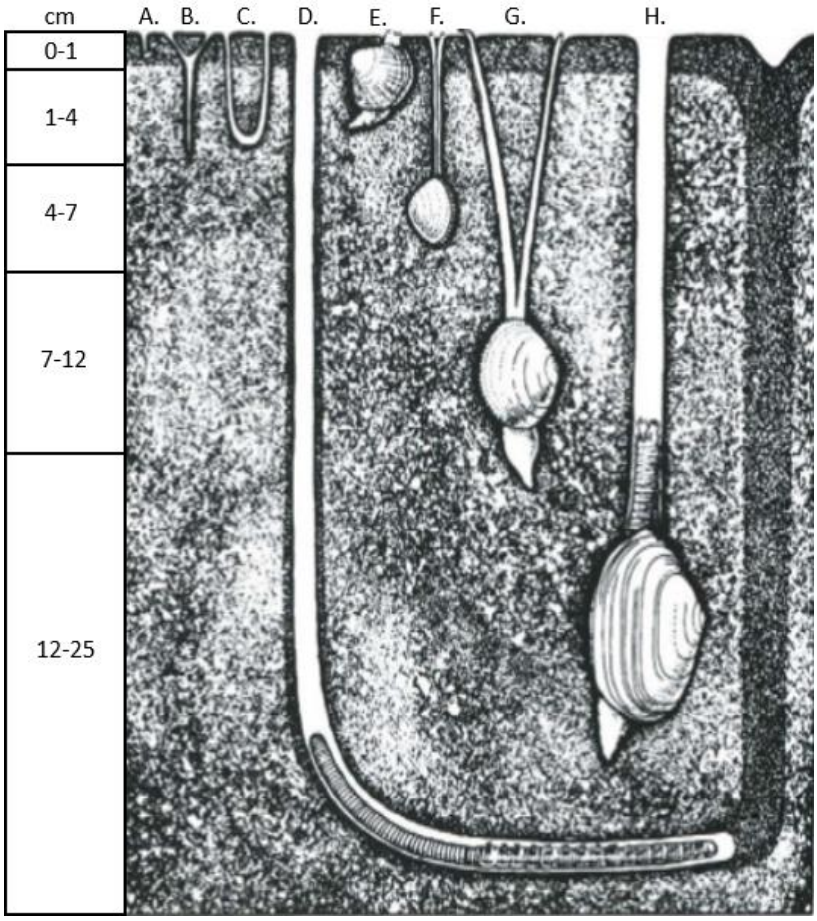

Figure 1.3: Representative infauna, showing their burrows and living depths. Examples include but not limited to (A) *Hydrobia*, a snail; (B) *Pygospio* burrow, a polychaete; *Corophium* burrow an amphipod; *Arenicola*, a polychaete; and clams (E) *Cardium*, (F) *Macoma*, (G) *Scrobicularia*, and (H) *Mya*. Original figure from Steele *et al*. (2001).

There has been an increased use of spatial scale incorporated into benthic ecology studies beginning in the 1980's based off a literature review by Ellis & Schneider (2008). Many studies have centralized on the large/landscape scale of spatial patterns of soft sediment intertidal species (commonly dominated by polychaetes and bivalves), influenced by the conventional knowledge that large-scale physical factors (temperature, salinity, tidal currents, sediment dynamics etc.) determine the distribution of intertidal species (Chapman, 2000; Legendre *et al*., 1997; Underwood & Chapman, 1996; Ysebaert & Herman, 2002). For example, sediment type is a determining factor of the distribution of intertidal macroinvertebrates where species have optimal preferences for sandy or muddy sediments or can live amongst both substrate types e.g. the suspension-feeding bivalve *Abra alba* prefer muddy fine sand, the polychaete *Nephtys cirrosa* prefer well-sorted sand and the bioturbating tunnelling-mud crab *Austrohelice crassa* can be distributed across both sandy and muddy sediment (Needham *et al*., 2010; van Hoey *et al*., 2004). Additionally, the subtidal zone has fast tidal current that result in low sediment stability are generally limiting, resulting in higher macrobenthos abundance and biomass in the intertidal zones than that of the subtidal (Ysebaert *et al*., 2003). Conversely, distinctive biological processes (e.g. inter- and intra-specific interactions) have small-scale effects that result in spatial patterns which are not identifiable at larger scales (Thrush, 1991; Thrush *et al.*, 1994; Underwood & Chapman, 1996). For example, the impact of the horseshoe crab, *Limulus Polyphemus*, on the clam, *Gemma gemma*, was assessed through a predator exclosure experiment. *G. gemma* were aggregated when protected from *L. polyphemus* and distributions were more random in unprotected plots, likely generated by an increase in mortality (Botton,

1984). Another biotic response forming these spatial patterns is self-organisation behaviour, which is often seen in many intertidal communities.

1.2 Self-organization behaviour

Growth and mortality are typical density-dependent mechanisms that occur in environments which are resource limited (e.g. food, space or water) driving self-organized spatial patterns in communities (Brook & Bradshaw, 2006; Rietkerk & van de Koppel, 2008). Alternatively, stress divergence of physical stressors (e.g. wave energy, desiccation) is another mechanism that can form self-organized patterns in communities resulting in positive local feedback and negative feedbacks at a greater scale (Temmerman *et al*., 2007). These individual interactions can generate self-organized patterns when an active behaviour performed by organisms results in optimal densities which reinforce facilitation and resilience at a small scale through habitat modification, while competition or other growth restricting interactions inhibit conspecifics at a large-scale (van de Koppel *et al.,* 2005).

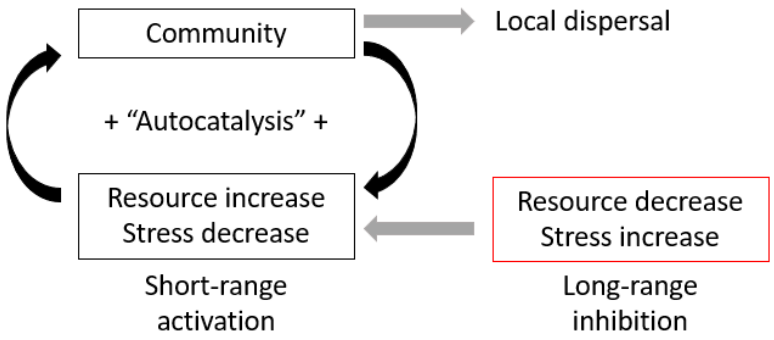

Figure 1.4: Scale-dependent feedback, where communities facilitate themselves by increasing resource availability and reducing stress leading to short-range activation. While causing long-range inhibition (competition), due to resources moving faster than communities and in an opposite direction, resulting in depleted resources moving further away. Figure adapted from (Rietkerk & van de Koppel, 2008)

An example is the formation of 'ridge and runnel' patterns of MPB in areas of strong tidal currents and 'round-shaped' patterns where tidal currents are weaker (Blanchard *et al*., 2000; De Brouwer *et al*., 2000). These patterns are related to diatom biofilms which are higher on elevated ridges or patches. These biofilms produce extracellular polymeric substances (EPS) that increases the cohesiveness and stability of sediment (Blanchard *et al*., 2000). Elevated ridges and patches experience increased drainage of water during tidal emergence which solidifies EPS, reducing erosion and promotes MPB growth. This results in a small-scale positive feedback between sedimentation and diatom growth which increases sediment surface elevation of up to 2 cm (Rietkerk & van de Koppel, 2008; Temmerman *et al*., 2007). This formation leads to the divergence of water into lower areas, forming runnels. These runnels remain consistently wet, preventing the accumulation of MPB, thus at larger scales negative feedback occurs due to the divergence of water into runnels (Figure 1.5).

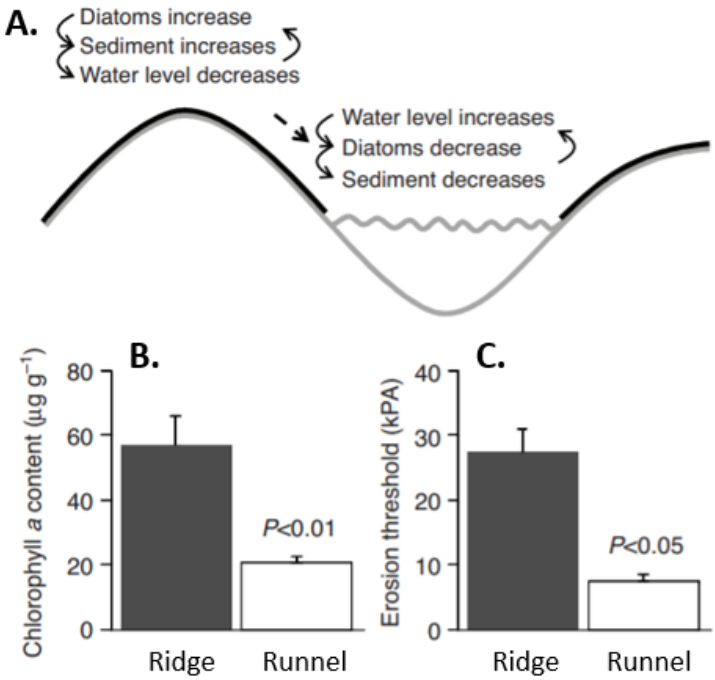

Figure 1.5: (A) Summary of diatom abundance, sediment dynamics and water level interactions. (B) Graph presenting greater diatom abundance on ridges than runnels. (C) Graph showing that sediment stability is greater on ridges than runnels. Original figure from van de Koppel *et al*. (2012).

Another example of a self-organised pattern is the formation of meadows by the seagrass, *Zosetera noltii*, which are organized in uniform interspaced banded patterns. The bands re organised perpendicular to tidal flow and have mean patch sizes ranging from 0.1 – 0.9 m^2 (van der Heide *et al*., 2010). These patterns formed due to a short-term positive feedback where high root density increases sediment stability and anchoring therefore lowers the risk of uprooting and mortality (Peralta *et al*., 2005). However, above the sediment surface a long-term negative feedback occurs where seagrass shoots are impacted by hydrodynamics resulting in the abrasion of the sediment on the coastward side, leaving an asymmetric depression preceding the seagrass band (Figure 1.6). An increase of shoot erosion of the coastward side occurs due to the depression depth and seagrass root depth being around the same (Figure 1.6). The depression depth is positively correlated with plot width and shoot density (Figure 1.6), acting as a long-term negative feedback (van der Heide *et al.,* 2010).

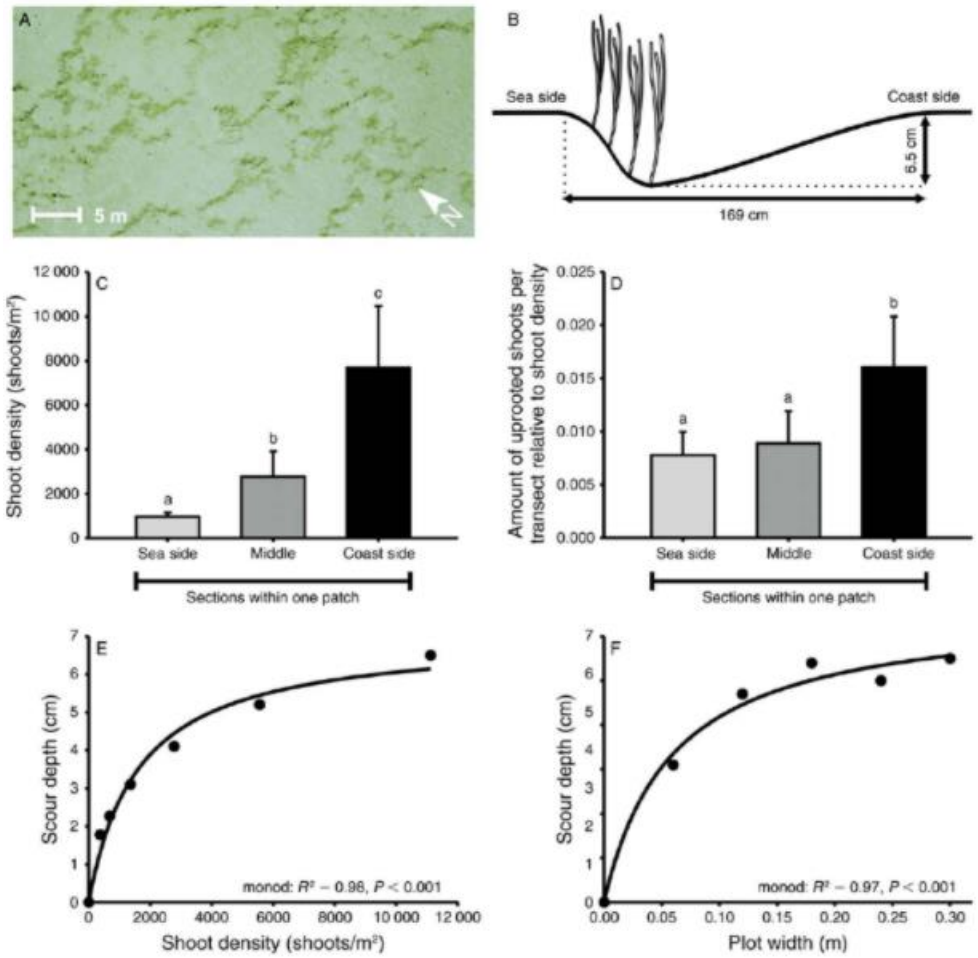

Figure 1.6: Measured characteristics of seagrass bands. (A) Aerial photograph of banded seagrass pattern at low tide. (B) Schematic cross-section showing asymmetric depression characteristic of seagrass bands. (C) Graph showing increased shoot density and (D) uprooted shoots on the coast side. (E) Graph showing increased scour depth with shoot density and (F) plot width (van der Heide *et al*., 2010).

The universality of self-organized spatial patterns in a variety of contrasting ecosystems (Rietkerk & van de Koppel, 2008) implies self-organization is important universally in developing ecosystem functioning and resilience against the growing adverse anthropogenic activity (Silliman *et al.,* 2015), providing useful contributions to monitoring. Which is particularly important regarding suspension feeding bivalves which are important bioindicators of ecosystem change e.g. heavy metal contamination or sedimentation (Chandurvelan *et* al., 2015; Thrush *et al*., 2004).

1.3 Suspension-feeding bivalves

Suspension feeding bivalves are generally found in abundance throughout estuaries and harbours in New Zealand (Mortin & Miller, 1973) and many temperate estuaries globally and fundamentally influence the functioning of estuarine ecosystems. For example, they have indirect or direct effects towards neighbouring macrofauna as they can extend above the sediment surface which can modify bed roughness e.g. *Mytilus edulis* (c. 2.5 – 3 cm; van Duren *et al*. 2006), *Atrina zelandica* (c. 15 – 20 cm; Green *et al*. 1998) and to a lesser extent *Austrovenus stutchburyi* (hereafter *Austrovenus*) (c. 1 cm; Jones *et al*. 2011b). In high densities bed shear stress and bioturbation activity increase vertical mixing allowing the bivalves to resuspend MPB, providing the bed with an important food source (Jones *et al*., 2011b).

High density suspension feeding bivalve beds can also play a role in controlling eutrophication, by grazing on phytoplankton and inorganic particles from the system if phytoplankton turnover time is equal to bivalve population clearance time and is less than the residence time (Dame & Prins, 1998; Jie *et al*., 2001; Officer *et al*., 1982). Once organic matter is filtered from the system the nutrients are assimilated into biomass, excreted into the system as inorganic nitrogen (Woodin *et al*., 2016) and deposited into the sediment as larger sized aggregates in the form of faeces or pseudofaeces (particles that are less nutritious or in excess of gut capacity) (Hily, 1991; Newell *et al*., 2005; Ostroumov, 2005). Although, most of the biodeposit content is eroded and resuspended by tidal energy (Widdows *et al*., 1998), small amounts of biodeposit can however accumulate onto sediment which results in an increase of organic matter into the benthos (Zhou *et al*., 2006). This excess of nutrients into the benthos can act as a positive

feedback fuelling microbial processes thus indirectly facilitating bottom-up control of primary production e.g. Sandwell *et al*. (2009) and Woodin *et al*. (2016) both found that *Austrovenus* improved MPB activity through increased ammonium excretion, especially so in higher densities (Sandwell *et al*., 2009). Accordingly, suspension feeding bivalves have an important functioning by modifying the flux of material of the sediment-water interface and the usage of these materials by neighbouring benthic deposit feeders (Jie, *et al*., 2001). Notably, the soft sediment habitats where dominant suspension feeding bivalves reside are highly dynamic, forcing these species to form spatial patterns with their conspecifics in an attempt to reduce stress towards themselves.

1.4 Evidence of spatial patterns in bivalves

There has been limited research on the spatial pattern formation of bivalves with the most studied species in soft sediment environments associated with spatial self-organisation being the blue mussel (*Mytilus edulis*) (van de Koppel *et al*., 2005). At a small-scale *M. edulis* have shown to form various spatial patterns depending on overall *M. edulis* density ranging from isolated clumps to labyrinths due to behavioural aggregation (a process comparable to the physical process of phase separation) (Figure 1.7), homogeneous beds can also occur in the presence of high density beds (Liu *et al.,* 2013). At a larger scale banded patterns are observed, where the distance between each *M. edulis* band differs between 2 – 20 m (Figure 1.6) (Liu *et al*., 2013, 2014). By forming these regular patterns, a balance is made where optimal protection from mortality (e.g. predation or wave dislodgment) and optimal food availability is recognized, as presented by van de Koppel *et al*. (2008). For example, *M. edulis* beds that are orientated perpendicular to tidal flow have individuals that facilitate each other at a small scale as conspecifics act as a substrate for attachment with byssal threads (secretion used to aid

in attaching to substrate) (Trevor & LeBarbara, 2009, van de Koppel *et al*., 2008). This provides extra stability as van de Koppel *et al*. (2005) argued that there is greater wave activity at the front of *M. edulis* bed bands. At larger scales *M. edulis* compete for algae which affect intake and growth, especially so in individuals that receive water depleted in algal stocks (van de Koppel *et al*., 2005). These bands are not as structured due to less wave activity thus less need for attaching with byssal threads (Figure 1.7). A study by Bertolini *et al*. (2019) found that homogeneous and striped patterns where most resistant to water flow in a controlled flume experiment where nearly no movement or dislodgement occurred, compared to small clusters and 'sparse' patterns which showed higher dislodgment rates. This self-organizing behaviour has been linked to the dependence of movement speed of local *M. edulis* density (van de Koppel, 2008). At low densities *M. edulis* move fast and decrease movement speed when small clusters are formed. Though, large and dense clusters trigger fast movement again due to low food availability. The formation of patterns is a fast process, where experiments have shown that stable patterns can arise within a few hours (Liu *et al*., 2013).

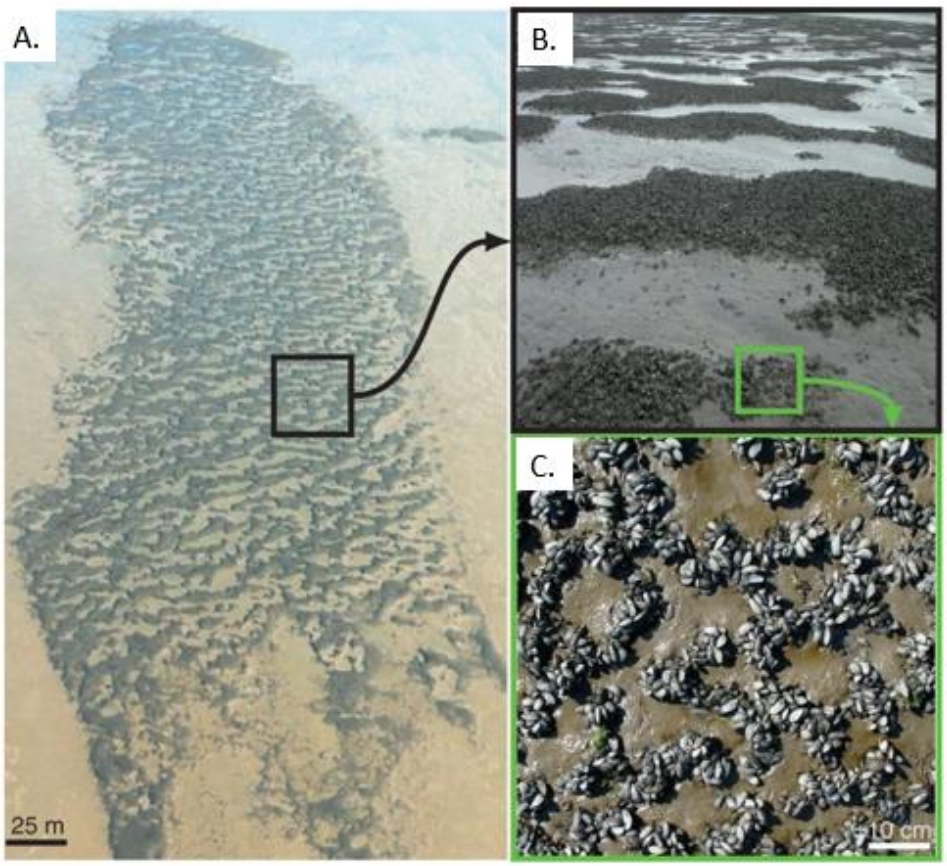

Figure 1.7: Spatial patterns of a self-organized *M. edulis* bed at two spatial scales enclosed within each other. A. Aerial view of a *M. edulis* bed with a width of 200 m. B. Banded patterns within the bed, successive *M. edulis* bands are at intervals of 2 – 20 m. C. Small-scale clusters situated within the bands (<20 cm). Original image from Liu *et al*. (2014).

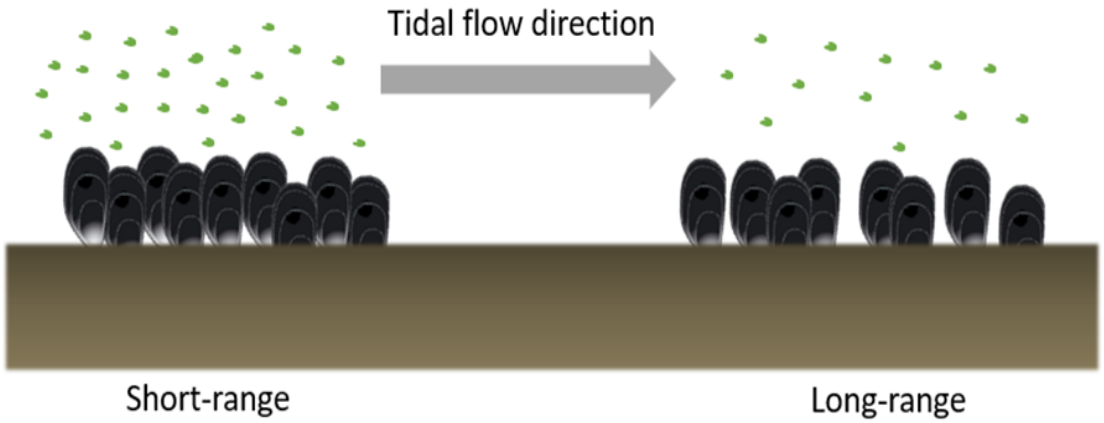

Figure 1.8: Summary of the short-range facilitation and long-range inhibition of mussel beds. Image adapted from van de Koppel *et al*. (2005).

Unlike the epibenthic blue mussel, *M. edulis,* which spatial patterns have been extensively studied for, *Austrovenus* is an infaunal bivalve in which spatial patterns are

not readily distinguishable. Landscape-scale studies have consistently noted that key infaunal suspension feeders have patchy distributions across intertidal flats e.g. Boldina & Beninger (2013) found that *Cerestoderma edule* an infaunal bivalve with equal functional roles as *Austrovenus*, presented clustered aggregations at <300 m (especially at the 0 – 60 m range) to kilometres. A study by Kraan *et al*. (2009) found *C.edule* to demonstrate a patch with a spatial range of 2000 m. Additionally, Huxham & Richards (2003) recorded *C.edule* exhibiting a patch with a spatial range of 20 m^2. Finer scaled spatial patterns of infaunal species are currently understudied (Ellis & Schneider, 2008). Hewitt *et al*. (1996) used 6 m as the upper scale of their sampling design and recommended a scale of < 5 m as this scale would be where individual crawling movement and inter-individual interactions were conceived to be influential. Hewitt *et al*. (1996) then found that adult *Austrovenus* demonstrated spatial structuring at small scales where clustering has shown to form a 1.3 m diameter patch nested within a 3 – 3.7 m diameter patch with additional smaller-scale patches of 30 cm within 2 – 2.7 m for juveniles. Contrary, Richardson *et al*. (1993) found that adult *C.edule*, were randomly distributed within maximum scales of 1 m^2, however sampling only occurred in two sites both with low *C.edule* densities.

Small-scale spatial patterns of *Austrovenus* have been persistent over a spatial and temporal scale (Hewitt *et al*., 1996, 1997). This indicates that spatial patterns of *Austrovenus* are not solely influenced by temporally variable factors, and that biological factors are of more importance (Hewitt *et al*., 1996, 1997; Schneider, 1991). Hewitt *et al*. (1996) demonstrates this where patch sizes were highly driven by individual mobility and have been exhibited in different size classes, denoting a continuum between behaviour and patch size. However, Legendre *et al*. (1997) has indicated that larger sized

Austrovenus distinctly exhibit spatial structures whereas smaller *Austrovenus* spatial structures are less spaced-out and are often influenced by physical variables e.g. wind-wave disturbances and tidal regimes. Although spatial patterns of *Austrovenus* (and similar functioning infaunal bivalves) have been studied at both large and to a lesser extent small-scale, it is currently unknown whether the distributions form unique patterns at different densities and environmental conditions or what is promoting the species aggregations to be resilient across space and time.

1.5 Study objectives

Heterogeneity is recognized as an important concept to incorporate into spatial ecology research. However, most small-scale studies conducted on spatial patterns of infaunal bivalves have been within 1 – 2 sites, these homogeneous sites are typically favored to reduce confounding effects of spatial heterogeneity (Lovett *et al*., 2005). Examples include Hewitt *et al*. (1996) and Richardson *et al*. (1993) all of which focused their studies on two to three sites respectively. Lovett *et al*. (2005) explained that to comprehend the relationships between spatial heterogeneity and ecosystem processes it is particularly important when: it is essential to recognize the average rate of a process across landscapes that are spatially heterogeneous and when researchers desire to know or predict process rate spatial patterns, by using the variations of spatial patterns and/or scales as response variables. Thus, instead of perceiving spatial heterogeneity as a confounding factor in spatial ecological studies, researchers should incorporate heterogeneity and see it as an opportunity to further understand the fundamental processes that control ecosystems. Furthermore, sampling plots of differing densities is important as density is an important driver for self-organized patterns resulting in optimal local densities and conspecific facilitation and survival (de Jager *et al*., 2017; Liu,

et al., 2013; van de Koppel *et al*., 2008). Additionally, translocation experiments also provide a way to investigate spatial pattern formation in a more controlled setting than that of natural beds, which can complement patterns observed from field studies.

Research on the spatial patterning of bivalves in translocation experiments is scarce and vastly understudied. van de Koppel (2008) performed a translocation experiment on *M. edulis*, where two densities of *M. edulis* (3.8 and 6.0 kg. m^{-2}) were translocated into a lab and placed on a homogeneous surface (60 x 30 cm) under controlled conditions to observe spatial pattern formation over time. Results found that in 24 h both treatments displayed "labyrinth-like" patterns (more so in the higher density treatment) which reflected natural *M. edulis* beds. Although studies have used translocation of *Austrovenus* as a basis of study (e.g. Sandwell *et al*., 2009), spatial patterning of this species under translocation conditions is not presently understood.

By using a field survey, I tested whether small-scale spatial patterns of *Austrovenus* are correlated with environmental variables and/or are density dependant. In summer of Dec – Feb (2019 – 20) I sampled for *Austrovenus* spatial structure in 4 m^{-2} plots which were replicated three times in low, medium and high densities at nine known *Austrovenus* beds to distinguish if spatial structure in natural beds occurs at small scales, whether these structures are density dependent and whether it varies with heterogenous environmental conditions. 4 m^{-2} plots were used as it is < 5 m which Hewitt *et al*. (1996) suggested for recognizing behavioural effects of adult *Austrovenus* and made logistical sense in allowing sampling to be replicated three times within one tidal cycle at a site.

In winter 2020 a follow up translocation experiment was performed where nine plots consisting of equal amounts of low, medium and high-density *Austrovenus* were planted in a homogeneous substrate. These plots were left for six weeks to distinguish if the spatial pattern formation was density dependent. The results provide novel insight on the behaviour of whether *Austrovenus* form spatial patterns which is important in understanding how these crucial ecosystem habitats persist over time and how this knowledge can be incorporated in restoration and conservation of these naturally occurring habitats.

The specific goals for this research were:

1. Do *Austrovenus* exhibit a spatial distribution that is significantly different to a random patterning within their natural environment depending on low, medium or high ambient densities?
2. Do *Austrovenus* exhibit a spatial distribution that is significantly different to a random patterning within their natural environment depending on environmental factors?
3. Do transplanted *Austrovenus* beds exhibit a spatial distribution that is significantly different from a random patterning with differing density treatments?
4. Does the plot scale density of translocated *Austrovenus* influence sediment conditions?

1.6 Research significance

Bivalve populations have shown a dramatic decrease worldwide due to overfishing and habitat degradation particularly areas adjacent to anthropogenic activity (Gibson *et al*., 2007; Jackson *et al*., 2001; Lotze *et al*., 2006). This is also reflective in *Austrovenus* densities in New Zealand which are decreasing due to overharvesting and extensive

sedimentation and pollution which have adversely modified soft-sediment habitats (Stewart & Creese, 2002; Cummings *et al*., 2007). Depletion of this species could consequently have considerable impacts on benthic-pelagic coupling and therefore productivity and functioning (Thrush *et al*., 2006) as *Austrovenus* is a major macrofaunal species of New Zealand intertidal estuarine environments. Therefore, the increased ecological knowledge obtained from this study will support in further understanding the role *Austrovenus* has on ecosystem biodiversity, functioning, productivity and the bed resilience of *Austrovenus*, focusing on small-scale patterns. The mechanistic understanding of the roles *Austrovenus* plays would not only be progressed but can also aid in conservation and restoration of these major habitat-engineers and creating better techniques in culturing to improve yield. This is important as restoration methods are typically direct. For example, disturbed areas can be too distant from a larval source to allow natural colonization and direct re-seeding of *Austrovenus* is obligatory for the bed's restoration (Jones *et al*., 2018; Lundquist & Pilditch, 2006). This knowledge can also potentially be transferred to other similar species of infaunal suspension feeding bivalves.

Chapter 2

Methods

2.1 Study species

Austrovenus stutchburyi or tuangi is an endemic New Zealand cockle and is a shallow-burrowing (2 – 3 cm) suspension-feeding bivalve that populates intertidal sediments of sheltered estuaries that are composed of mud to coarse sand (Morton & Miller, 1973). Peak abundances occur in sandy sediments with a low mud content and typically abundances decrease with increasing mud content (Ellis *et al*., 2017). *Austrovenus* migrate short distances per day (up to 30 cm in a single tidal cycle) using oscillatory foot movement as a response to the surrounding environment (Mouritsen, 2004). Larger *Austrovenus* however are relatively sessile, as post settlement movement is not as essential as juvenile dispersal (Norkko *et al*., 2001). Infaunal bivalves have shown to only move to improve development and growth conditions (e.g. shift to maximize food availability) (Beukema, 1993) and avoid adverse local conditions (e.g. contaminants) (Pridmore *et al*., 1991). *Austrovenus* is a key species in New Zealand estuaries often accounting for the majority of intertidal macrofaunal biomass. At high densities (up to 4500 m^{-2}) (Singleton *et al*., 2013) they enhance nutrient fluxes and benthic primary production as well as acting as a food source for higher trophic level species (Adkins *et al*.,, 2014; Jones *et al*., 2017; Sandwell *et al*., 2009; Thrush *et al*., 2006). Adult *Austrovenus* can grow up to 60 mm in length (Powell, 1979) but in Tauranga Harbour they are generally < 40 mm with size classes between 5 – 20 mm being the most common (Ellis *et al*., 2017).

2.2 Study site description

Tauranga Harbour (37°36’ S, 176°03’ E) – known by Te Awanui to the local iwi, is a large tidal estuary (218 km^2) located in the western Bay of Plenty, New Zealand. The harbour is protected from the Pacific Ocean by a large barrier island (Matakana Island) and two Holocene barrier tombolos at the northern (Bowentown) and southern (Mt Maunganui) entrances (Figure 2.1).

There are two harbour basins which are separated by intertidal flats in the central region and although they are physically connected, water exchange is limited between the two (Tay *et al*., 2012). At mean high water the northern basin has an approximate volume of 178 million m^3 with the southern basin having 278 million m^3 (Park, 2009). The harbour is mainly shallow (< 10 m depth), with approximately 66 % of the total area being intertidal flats (Park, 2004). Numerical models have estimated that the residence time of the estuary ranges from 3 to 8 d with higher residence times in sub-estuaries and constricted mouths (Tay *et al*., 2013).

The surrounding catchment of the harbour is extensively used for horticultural and agricultural purposes and urban use particularly in the southern basin where Tauranga City is located (Lawton & Conroy, 2019). The harbour is also a traditional source of food for the residents of Bay of Plenty, where fish and shellfish are often collected as a recreational activity.

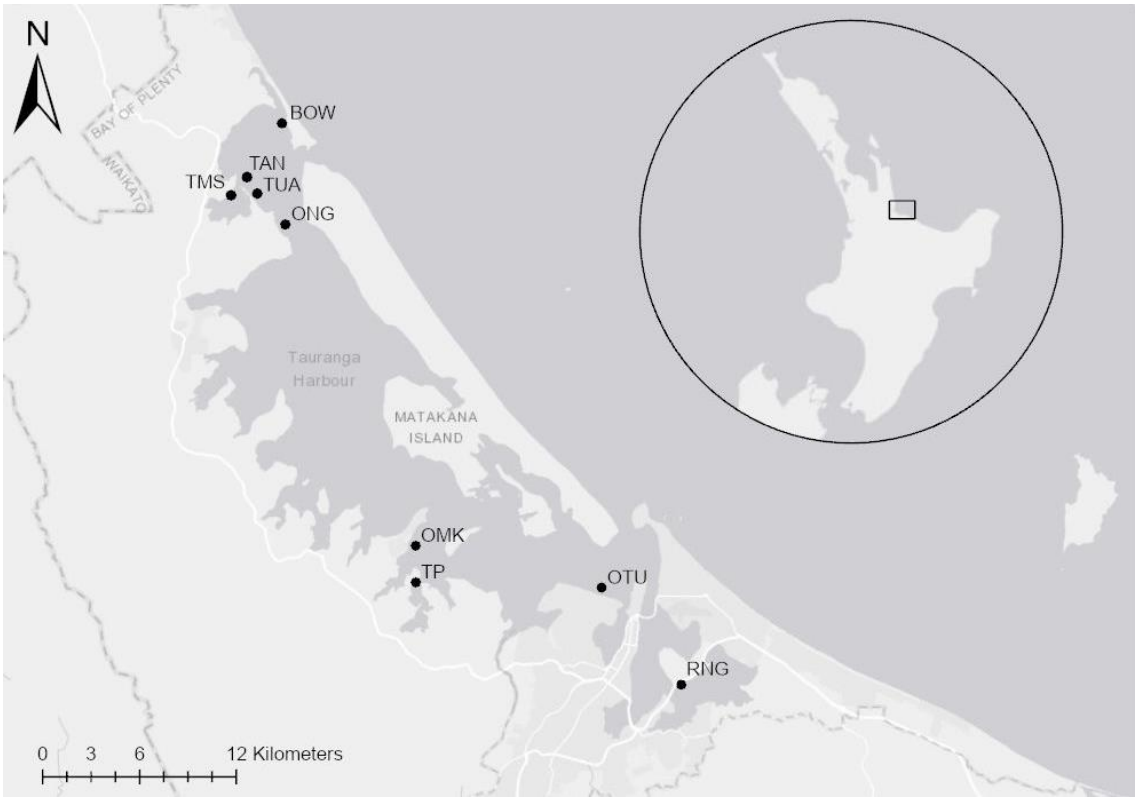

Figure 2.1: Map of Tauranga Harbour showing locations of the nine sampling sites in the field survey.

2.3 Sampling design

2.3.1 Field survey

Field survey sampling occurred from December 2019 to February 2020 at nine predetermined *Austrovenus* beds in Tauranga Harbour (Figure 2.1). The reason for sampling at multiple sites was to see if spatial structure of *Austrovenus* was correlated with density and influenced by sediment grain size. At each site a 4 m^2 plot was established in a 'low', 'medium' and 'high' density (abbreviated as L, M and H respectively on the site code) aggregates of *Austrovenus*. The aggregate density was relative and estimated by taking preliminary core samples in the proximity of the plot. A 13 cm diameter PVC core was used to extract the macrofauna samples to a depth of 15 cm or until clay or bedrock was reached. Core samples were taken at 0.5 m intervals within the plots and at 1 and 2 m intervals from each side of the plot which were lined

along and across shore to check for anisotropy (direction-dependent variation of spatial characteristics) (Figure 2.2). Samples were then sieved on a 1 mm mesh and both juvenile and adult *Austrovenus* were removed, placed in a sorting tray with a scale and photographed, they were then returned to the sediment to ensure the experiment remains non-invasive (Figure 2.3). The photographs were used to count and measure *Austrovenus* using ImageJ, a photo analysis program (Schneider *et al.,* 2012). Sediment samples were taken with a 25 mm diameter syringe core to a depth of 5 cm in five random locations within each plot while avoiding dedicated macrofauna core points. These five samples were pooled and stored in sediment bags for ease of homogenisation.

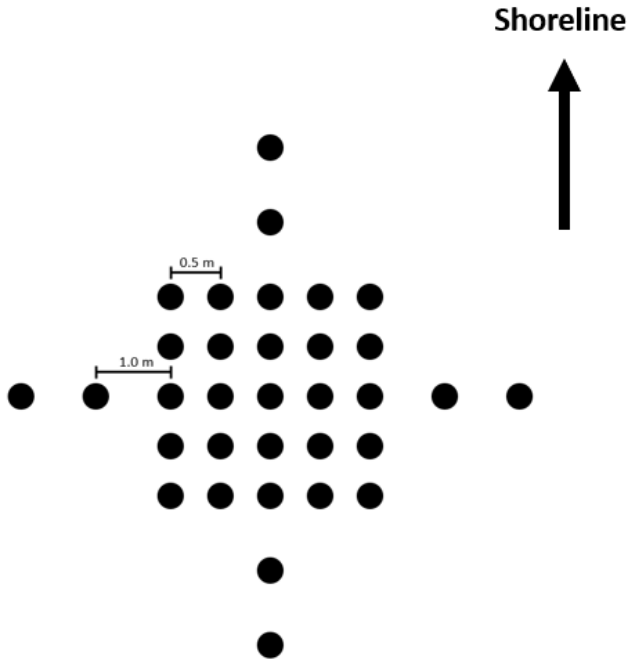

Figure 2.2: Sampling plot covering 4 m^2 showing the core (diameter = 13 cm) locations used to assess spatial structure of *Austrovenus.* A total of 25 samples were taken within the plots and a further eight samples outside the plots.

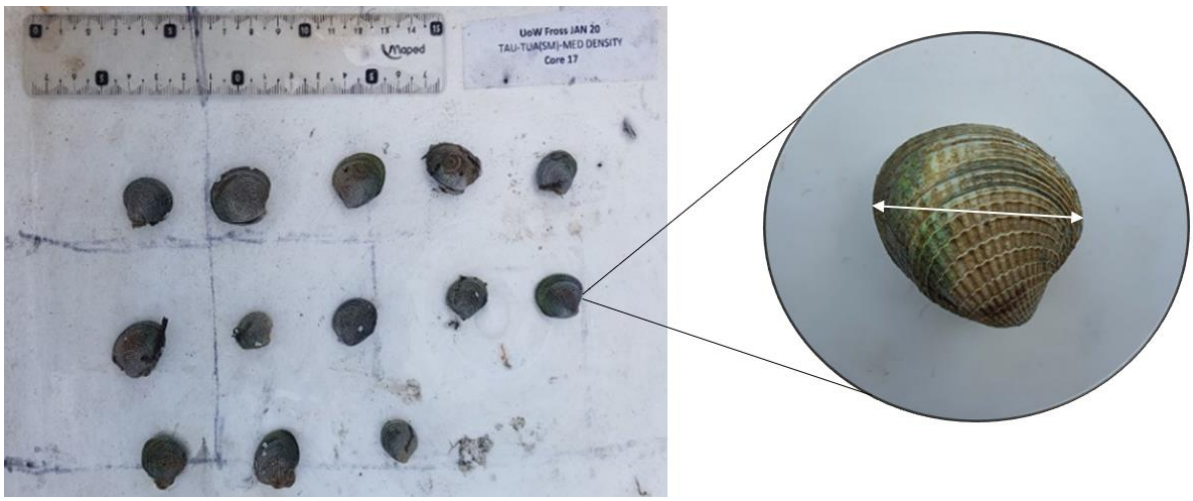

Figure 2.3: Photograph of *Austrovenus* placed in a tray to be analysed for size and abundance in ImageJ. Measured shell dimension is displayed on the right.

2.3.2 Translocation experiment

In order to assess *Austrovenus* behaviour in a region of low ambient densities and whether this resulted in structured patterns a translocation experiment was conducted. Translocation was done on the 18th of June 2020 at Tuapiro Point (TUA), Tauranga Harbour (Figure 2.1). *Austrovenus* were transferred from an established cockle bed on the exposed region of Tuapiro Point to a site that had low ambient densities (~2.5 ind. core^{-1}) on the sheltered region (Figure 2.4). This was done to have control over the three density groups and to observe if *Austrovenus* left or alternatively been recruited into the plots. Adult *Austrovenus* were extracted by finger ploughing and sieved with 500 µm sieves, they were then counted based on a known volume of 1000 individuals in marked buckets. This option was used to reduce the time required to complete the translocation rather than counting each individual. Plots were randomly distributed at the translocation site while also being at least two metres apart to prevent any influence between the plots.

Three *Austrovenus* density plots of 4 m^2 were chosen, 800 m^{-2} (low), 1600 m^{-2} (medium) and 2500 m^{-2} (high). Individual *Austrovenus* were uniformly spread within each plot each

density treatment was replicated three times (Figure 2.5). These plots remained in-situ for six weeks and were sampled between 30th July and 1st August 2020. The plots were sampled for biological and environmental variables with the same sampling design as the field survey experiment (Figures 2.2 & 2.3). Three random plots in the adjacent area were additionally sampled to quantify the ambient *Austrovenus* abundance and environmental variables of the translocation site.

Figure 2.4: Map of Tuapiro Point showing the key locations of the translocation experiment, (A) being the original *Austrovenus* bed and (B) being the site where *Austrovenus* were translocated to. Refer to Figure 2.1 for the general location of Tuapiro Point (TUA).

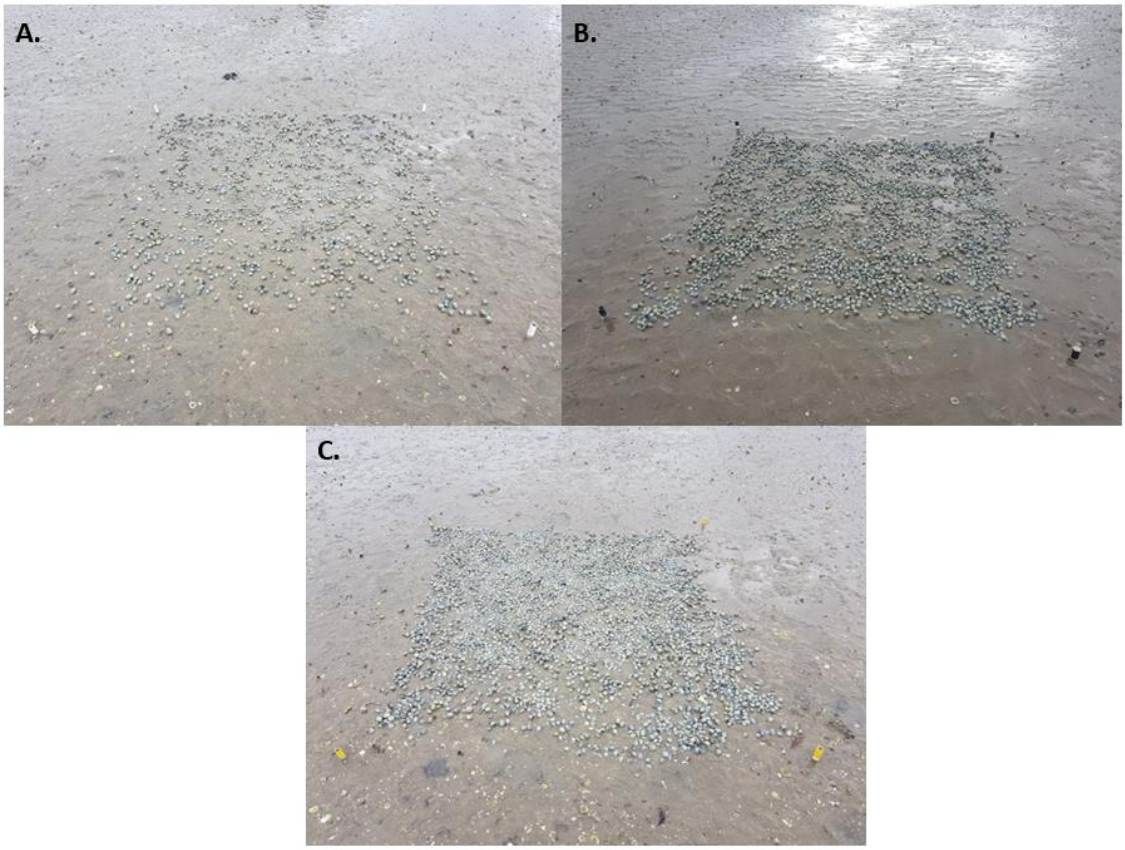

Figure 2.5: Low (A), medium (B) and high (C) densities of translocated *Austrovenus* plots.

2.4 *Austrovenus* variables

Austrovenus abundance and size were analysed in ImageJ. Each image was calibrated to 10 mm by using the ruler for scale from each image. A trial was performed on the accuracy of measuring *Austrovenus* in ImageJ, where 20 individuals of differing sizes were measured with callipers and then compared with the measurements in ImageJ (refer to Figure 2.3 for maximum shell dimensions). The results of this trial showed that ImageJ was an accurate program to use for measuring and counting *Austrovenus* as a maximum difference of 2.0 mm from the predicted measurements was observed (Figure 2.6). Average abundance and size groups of the total *Austrovenus* and those >10 mm (adults) was derived. This was important as juveniles and adults have different degrees of mobility, where juveniles are more likely to be transported with tidal activity

compared to adults (Hewitt *et al*., 1997), and thus may affect the strength of spatial autocorrelation within the plots when included. The translocation experiment did not require this separation of adult and juvenile *Austrovenus* as most individuals were mature (>10 mm) with little to no juveniles being recorded.

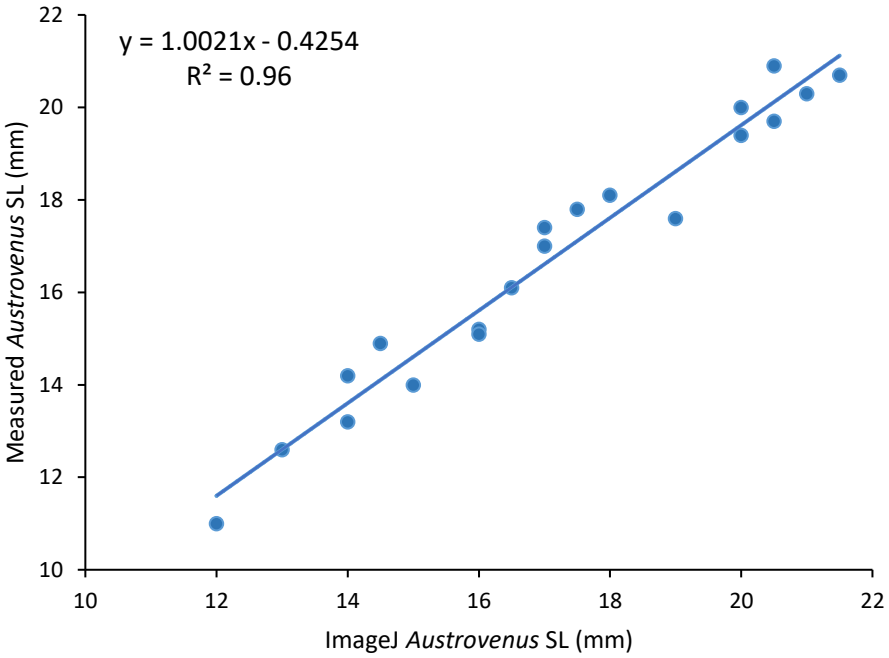

Figure 2.6: Regression of observed vs predicted Austrovenus SL in the trial experiment of ImageJ accuracy.

2.5 Environmental variables

Sediment samples were kept on ice and in the dark to prevent any changes in chlorophyll *a* (chl *a*) or organic matter content (OM) then frozen at -20 °C until analysis. Once thawed, each sample was manually homogenised in the sample bags and divided into three subsamples corresponding to grain size chlorophyll *a* and phaeopigment and organic matter. Sediment chl *a* and phaeopigment (phaeo) content was acquired by freeze drying the samples for three days to remove any moisture from the samples before homogenising and subsampling. Of the freeze-dried material a 0.15 g subsample was then extracted in 10 mL of 90 % buffered acetone which was steeped for 24 h at

4 °C. Then fluorescence was analysed before (for chl *a*) and after acidification of 1mL hydrochloric acid (for phaeo) on a Turner Designs 10-AU Fluorometer (Arar & Collins, 1997). The pigments were reported as μg g^{-1} dw sediment. Sediment OM was measured by percent weight loss on ignition of a 10 g sediment sample that was dried (60 °C for 72 h) and ashed (550 °C for 4 h). The difference in weight between the two drying temperatures was then calculated as sediment OM content (Heiri *et al*., 2001).

Sediment for grain size analysis were pre-treated by filling a beaker halfway with 10 % hydrogen peroxide and were topped up every 2 – 4 d for three weeks, to allow the OM content to be removed and aid in breaking up flocculation (Gray *et al.,* 2010). Sediment median grain size (Med GS) and mud content (% of particles <63 μm) was derived from a MALVERN MASTERSIZER-S where particle grain size distribution was measured on a volume basis and calgon was added to aid in particle dispersion (Singer *et al*., 1988).

Site exposure (E_M) to wind-wave activity was calculated by following the method described by Turner *et al*. (1999). For each summer period (Dec – Feb) between 2007-2017 monthly mean wind speed and frequency of occurrence in 30° wind direction bins was extracted from Bay of Plenty Regional Council wind speed records (recorded at 10-minute. The fetch (distance to nearest land mass) at each 30°interval was estimated from Google Earth and the following equation then used to calculate a summer wave exposure score (E_M):

$$E_M = \sum_{i=1}^{4} mean\ wind\ velocity_{30i^\circ} \times Percent\ frequency_{30i^\circ} \times fetch_{30i^\circ}$$

Mean wind velocity = mean monthly wind speed in m s^{-1} for each bin over the 10-year summer period. Percent frequency = percent frequency in which the wind occurred from

each direction bin over the 10-year summer period. Fetch = distance from each site to land mass along any given bin increment. As all translocation plots were situated in the same site, wave exposure was not estimated due to no variability between the plots.

2.6 Statistical analysis

Pearson's correlation matrices were made in RStudio to determine relationships between *Austrovenus* and environmental variables. The response variables included mean average *Austrovenus* abundance and shell length (SL), while explanatory or environmental variables included Med GS; mud content; OM content; chl *a*; phaeo and wind exposure. Sharpiro-Wilks test was performed on variables to test for normality and a log+1 transformation was made if required, to meet the assumptions of Pearson's correlation coefficient. These correlations are important as they give an insight on whether variations of cockle density/size are correlated with environmental variables.

Spatial patterns of populations in space can be characterized as dispersed, clustered or random. Spatial autocorrelation is a method used to assess the dependence of the number of individuals in one sample being similar to that of the numbers in neighbouring samples, ruling out the factor of chance (Legendre, 1993). Patterns can be interpreted and variation covering multiple scales quantified statistically with Moran's *I* (Boldina & Beninger, 2013; Legendre & Fortin, 1989). Additionally, autocorrelation supplements the statistical validity of patterns and reinforces ecological inferences (Kraan *et al*., 2013; Thrush, 1991; Wagner & Fortin, 2005). Moran's *I* values can range from -1 to +1, values closer to -1 denote more dispersed patterns, values close to 0 denote random patterns while values closer to +1 denote clustered patterns. It is expected that *Austrovenus* will present a Moran's *I* of around 0 – 1 as the species is a

suspension feeder reducing competition for surface space unlike deposit feeders which are usually dispersed (Holme, 1950). The Moran's *I* statistic was calculated in ArcGIS Pro 2.6 using the geoprocessing tool "Spatial autocorrelation" at a distance threshold of 0.5 m to ensure each point had at least one neighbour. Subsequent contour plots to assist in interpreting spatial patterns were produced in RStudio 1.3.1093 using the "Plotly" package. This was done for the total abundance and those >10 mm to distinguish any differences in spatial distribution when juveniles were included or excluded. Size class groups greater than 15, 20 and 25 mm were also explored but excluded from the results as no distinct spatial pattern was observed.

Quantile regression models of the 95th abundance percentile were fitted across environmental gradients and were made in JMP Pro 15.2.1. This type of regression was completed by separating each of the environmental gradients (Med GS, mud content and wave exposure) into 3 – 4 bins where the 95th percentile abundance of *Austrovenus* is calculated in each bin. This was used to examine the effects of environmental variables in limiting the maximum abundance of *Austrovenus*. A polynomial model was then fitted to the data, using the 95th percentile abundance in each bin as the dependent variable. Med GS, mud (%) and wave exposure were included as the independent variables in the polynomial model. A second set of quantile regressions were performed to assess the influence of *Austrovenus* abundance on OM, chl *a* and phaeo content of the sediments. In this case the environmental variables were treated as the dependant variable.

Chapter 3

Results

3.1 Field survey

3.1.1 *Austrovenus* and environmental variables

Sampling occurred across a density gradient and from the site sedimentary variables there was also evident sediment gradient present (Table 3.1). Mud % is a proxy for increasing sediment derived from terrestrial inputs while OM content is the settlement of biogenic material that has originated from marine primary production. OM content and mud % were positively and significantly correlated (R = 0.73; p = <0.001; Table 3.2) where an increase in OM content was related to an increase in mud %. OM content ranged from 1.4 to 5.1 % and mud % ranged from 1.2 to 21.8 %. Med GS (although not as strong as the correlation between OM content and mud %) was also correlated with mud % (R = -0.49; p = 0.010; Table 3.2), which showed a decrease of 117 µm from the least muddy site (OTU-L = fine sand) to the muddiest site (ONG-M = slightly muddy-sand). Med GS was negatively correlated with *Austrovenus* SL (R = -0.55; p = 0.003; Table 3.2), where an increase in Med GS resulted in a decrease of *Austrovenus* SL. Wave exposure was also shown to positively affect *Austrovenus* SL (R = 0.62; p = <0.001) as sites that had greater wave exposure were associated with larger *Austrovenus* individuals (Table 3.2). None of the environmental variables were correlated with wave exposure however trends did exist with more course grained sediment and a decrease in mud %, OM content and pigments at exposed sites (Table 3.1).

Chl *a* ranged from 5.3 (BOW-L) to 28.4 µg g^{-1} dw (ONG-M) (Table 3.1) and was correlated with mud % (R = 0.57, p = 0.002) and OM content (R = 0.74, p = <0.001) (Table 3.2). Phaeo ranged from 1.1 (OTU-H) to 16.3 µg g^{-1} dw (ONG-H) (Table 3.1) and was also correlated to OM content (R = 0.45, p = 0.018; Table 3.2).

Austrovenus abundances ranged from 2 to 43 ind. $core^{-1}$. There was no correlation between *Austrovenus* total and >10 mm abundances and environmental variables based on a linear correlation (p = >0.05; Table 3.2). However, based on the 95th percentile unimodal relationships between *Austrovenus* abundance and environmental variables was evident (Figure 3.1). Med GS increased with *Austrovenus* abundance until a critical value of around 270 µm where a decline begun to occur. Abundance of *Austrovenus* increased initially up to a critical value of 8 % mud after which they declined. Similarly, wave exposure increased *Austrovenus* abundance until around 4000 E_M where greater wave exposure caused a decline. These observations show that very muddy and/or wave exposed sites do not support high density of *Austrovenus.* Both OM content and chl *a* had similar trends where an increase of *Austrovenus* abundance to 10 ind. $core^{-1}$ caused OM content and chl *a* to increase. A decline of both variables occurred from 10 to 20 ind. $core^{-1}$ and abundances greater than 20 ind. $core^{-1}$ shown to have no further effect on OM content and chl *a* (Figure 3.1). Phaeo increased until around 20 ind. $core^{-1}$, abundances greater caused a linear decline (Figure 3.1). This shows that OM content and pigments are greatest at intermediate *Austrovenus* densities, however, begin to decrease with high densities.

Table 3.1: Summary of site-plot *Austrovenus* and environmental variables ordered from low to high mud content %. *Austrovenus N*: Mean *Austrovenus* abundance, *Austrovenus* SL: *Austrovenus* shell length, Med GS: median grain size, mud %: mud content, OM: organic matter, chl *a*: chlorophyll *a*, phaeo: phaeopigment. Bracketed values indicate the range.

Site	*Austrovenus N* (ind. core^{-1})	*Austrovenus* SL (mm)	Mud (%)	Med GS (µm)	OM content (%)	Chl *a* (µg g^{-1} dw)	Phaeo (µg g^{-1} dw)	Wave exposure (E_M)
OTU-(L)	7.8 (1-16)	15.7 (9.0-27.2)	1.2	231	1.4	6.9	4.7	4927
RNG-(L)	3.2 (1-9)	10.5 (7.1-16.4)	3.0	427	2.1	16.9	4.0	2402
TAN-(H)	26.4 (10-34)	20.2 (9.6-30.8)	3.5	200	2.9	8.2	2.7	9643
TAN-(M)	12.6 (3-27)	19.6 (8.4-28.4)	3.6	202	2.3	9.9	1.7	9614
BOW-(H)	23.3 (7-43)	17.5 (6.0-25.4)	3.9	358	1.9	8.1	3.3	4600
BOW-(L)	14.4 (5-39)	14.2 (6.5-23.0)	4.0	291	1.7	5.3	2.1	4433
TUA-(M)	17.8 (6-34)	19.9 (6.5-33.2)	4.1	173	2.7	11.0	5.4	6150
TUA-(L)	16.5 (2-36)	19.5 (5.9-29.3)	4.2	169	2.9	9.7	5.3	6142
OTU-(H)	16.9 (4-38)	19.8 (8.5-27.4)	4.9	204	2.2	11.5	1.1	4901
OTU-(M)	14.5 (8-31)	20.4 (9.0-29.0)	5.8	215	1.9	16.5	1.4	5091
TUA-(H)	31.7 (17-51)	20.0 (17.0-31.5)	6.1	181	2.7	10.5	5.3	6186
BOW-(M)	13.4 (4-32)	20.7 (7.0-29.7)	7.0	324	1.4	8.3	4.0	4367
TMS-(H)	43.0 (22-55)	18.3 (6.9-28.8)	7.1	343	4.2	17.5	6.7	2883
RNG-(M)	13.2 (4-57)	12.5 (5.0-21.0)	7.3	387	2.6	7.3	4.2	2569
TAN-(L)	11.6 (5-19)	17.2 (7.4-30.0)	8.9	196	2.7	10.7	2.9	9487
TMS-(L)	3.8 (1-9)	15.4 (7.4-23.3)	9.7	187	3.0.	7.2	3.7	2326
RNG-(H)	18.1 (3-39)	13.4 (4.4-21.7)	10.2	328	2.0	13.0	5.3	2472
TMS-(M)	13.6 (4-32)	19.8 (6.4-29.3)	10.9	187	3.1	8.2	2.7	2181
ONG-(H)	15.2 (4-24)	22.0 (13.0-33.0)	12.4	130	4.4	20.9	16.3	6909
OMK-(M)	4.5 (1-9)	19.9 (7.5-27.0)	12.7	177	3.0	15.3	3.6	5316
ONG-(L)	4.0 (1-24)	17.5 (8.5-24.0)	14.3	195	2.4	8.7	4.6	4538
TP-(H)	19.7 (5-36)	15.7 (6.1-22.2)	14.8	267	3.8	21.0	7.9	898
OMK-(H)	10.7 (4-19)	17.8 (5.5-28.0)	17.9	129	3.6	11.4	5.8	5287
TP-(M)	12.6 (9-31)	14.5 (5.1-21.6)	18.6	213	4.5	20.8	12.4	759
TP-(L)	8.6 (1-17)	13.7 (5.9-20.3)	18.8	147	4.6	24.4	5.2	684
OMK-(L)	6.0 (0-13)	19.0 (6.2-27.0)	20.3	134	3.3	14.1	6.1	5187
ONG-(M)	7.6 (2-13)	23.3 (8.1-34.0)	21.8	114	5.1	28.4	1.7	6375

Table 3.2: Pearson's correlation coefficients of *Austrovenus* and environmental variables. Correlations with significant p-values (<0.05) shown in bold. ln = natural log transformation, SL = shell length. Number of plots = 27.

	ln *N* (ind. core^{-1})	SL >10 (mm)	SL (mm)	ln Med GS (µm)	ln Mud (%)	ln OM content (%)	ln Chl *a* (µg g^{-1} dw)	ln Phaeo (µg g^{-1} dw)	Wave exposure (E_M)
ln *N* >10 mm (ind. core^{-1})	1	0.32	0.34	0.16	-0.21	0.04	-0.04	0.07	0.16
ln *N* (ind. core^{-1})		0.29	0.30	0.20	-0.25	0.02	-0.05	0.08	0.15
Med SL >10 (mm)			1	**-0.57**	0.05	0.15	0.09	-0.20	**0.62**
SL (mm)				**-0.55**	0.05	0.15	0.10	-0.19	**0.62**
ln Med GS (µm)					**-0.49**	**-0.55**	-0.31	-0.08	-0.36
ln Mud (%)						**0.73**	**0.57**	0.36	-0.32
ln OM content (%)							**0.74**	**0.45**	-0.19
ln Chl *a* (µg g^{-1} dw)								0.33	-0.36
ln Phaeo (µg g^{-1} dw)									-0.39

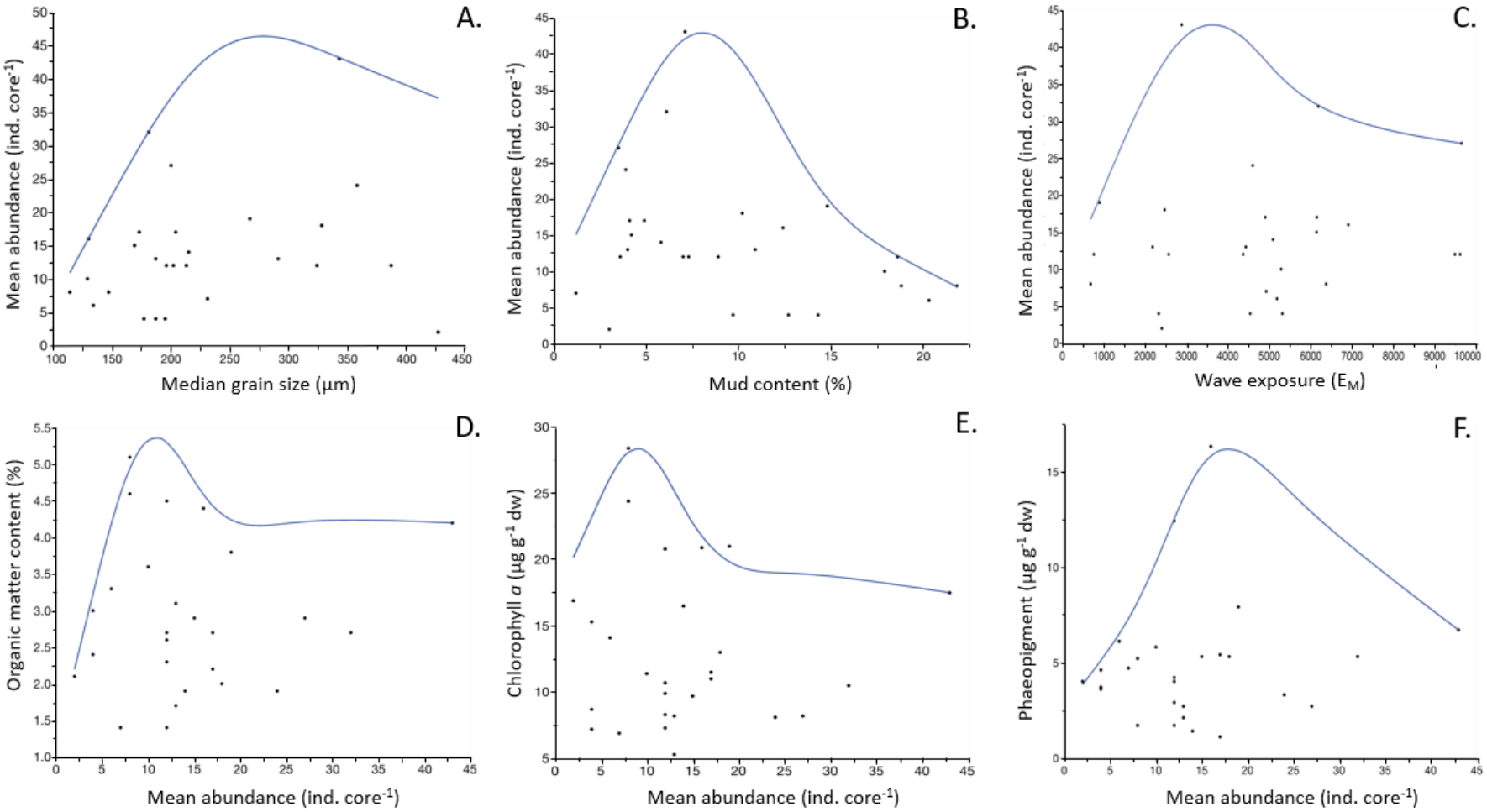

Figure 3.1: Relationship between *Austrovenus* abundance and environmental variables with a quantile regression (95th percentile) with knotted spline effect fitted. Top row: environmental variables expected to influence *Austrovenus,* whereas the bottom row is environmental variables expected to be influenced by *Austrovenus* abundance. (A.): Med GS; (B.): Mud content; (C.): Wave exposure; (D.): OM content; (E.): Chl *a*; (F.): Phaeo.

3.1.2 Spatial patterns

Overall, there was no clear spatial pattern of *Austrovenus* aggregations in all the plots sampled, with most sites/plots accepting the null hypothesis when the total abundance of *Austrovenus* was considered (except ONG-H, OTU-M, RNG-L and TMS-M). This indicates a random pattern of abundances within the sampled plots (Table 3.3). From inspecting the contour plots RNG-L had a large cluster of low abundance values and TMS-M had a large cluster of >14 ind. core^{-1} which resulted in the rejected hypothesis (Figure 3.2). Both ONG-H and OTU-M showed a dispersed pattern (Figure 3.2). There were no significant structured spatial patterns of *Austrovenus* aggregates between sites that shared low medium and high densities in relation to overall bed density, which can also be said for sites that shared similar Med GS and mud %.

Excluding the juvenile size classes (SL < 10 mm) and considering just the adults was the primary driver for influencing sites to reveal more spatial structure. When juveniles were excluded, the null hypothesis was rejected at an additional two locations OTU-L (dispersed) and RNG-H (clustered) and also a decrease in cluster size from RNG-L and TMS-M occurred. However, there was no clear distinction between a clustered or dispersed pattern as both positive and negative Moran's *I* values were observed (Table 3.4 & Figure 3.2). Although more sites rejected the null hypothesis when excluding <10 mm *Austrovenus* the majority of plots still displayed a random distribution.

Table 3.3: Global Moran's *I* statistics of describing the spatial structure of *Austrovenus* in sampled plots of nine sites, ordered in increasing site mud %. Rejected null hypothesis are indicated in bold. A rejected null hypothesis indicates that the spatial pattern of the samples is different from random and are either dispersed or clustered. The closer the Moran's *I* value is to -1 the stronger the dispersed pattern is, similarly the closer the Moran's *I* value to 1 the stronger the clustered pattern is.

Site	*Austrovenus N* (ind. core^{-1})	Moran's *I*	p-value	z-score
OTU-L	7.8 (1-16)	-0.256	0.148	-1.448
RNG-L	3.2 (1-9)	**0.320**	**0.012**	**2.499**
TAN-H	26.4 (10-34)	0.003	0.754	0.313
TAN-M	12.6 (3-27)	-0.266	0.123	-1.541
BOW-H	23.3 (7-43)	-0.216	0.243	-1.167
BOW-L	14.4 (5-39)	-0.035	0.963	0.046
TUA-M	17.8 (6-34)	-0.217	0.213	-1.245
TUA-L	16.5 (2-36)	-0.117	0.612	-0.508
OTU-H	16.9 (4-38)	-0.060	0.899	-0.127
OTU-M	14.5 (8-31)	**-0.318**	**0.062**	**-1.869**
TUA-H	31.7 (17-51)	-0.036	0.971	0.037
BOW-M	13.4 (4-32)	0.106	0.300	1.036
TMS-H	42.3 (22-55)	-0.195	0.278	-1.084
RNG-M	13.2 (4-57)	0.207	0.164	1.852
TAN-L	11.6 (5-19)	-0.021	0.892	0.136
TMS-L	3.8 (1-9)	-0.135	0.518	-0.646
RNG-H	18.1 (3-39)	0.211	0.185	1.720
TMS-M	13.6 (4-32)	**0.259**	**0.033**	**2.128**
ONG-H	15.2 (4-24)	**-0.284**	**0.099**	**-1.651**
OMK-M	4.5 (1-9)	0.162	0.172	1.365
ONG-L	4.0 (1-24)	-0.006	0.809	0.241
TP-H	19.7 (5-36)	-0.065	0.870	-0.164
OMK-H	10.7 (4-19)	-0.057	0.917	-0.104
TP-M	12.6 (9-31)	-0.090	0.727	-0.350
TP-L	8.6 (1-17)	-0.132	0.540	-0.613
OMK-L	6.0 (0-13)	0.079	0.414	0.817
ONG-M	7.6 (2-13)	-0.258	0.147	-1.450

Table 3.4: Global Moran's *I* statistics of describing the spatial structure of *Austrovenus* (>10 mm) in sampled plots of nine sites, ordered in increasing site mud %. Rejected null hypothesis are indicated in bold.

Site	*Austrovenus N* >10 mm (ind. core^{-1})	Moran's *I*	p-value	z-score
OTU-L	7.8 (1-16)	**-0.315**	**0.064**	**-1.854**
RNG-L	3.2 (1-9)	**0.206**	**0.091**	**1.689**
TAN-H	26.4 (10-34)	-0.001	0.773	0.289
TAN-M	12.6 (3-27)	-0.244	0.164	-1.392
BOW-H	23.3 (7-43)	-0.184	0.344	-0.946
BOW-L	14.4 (5-39)	0.018	0.662	0.438
TUA-M	17.8 (6-34)	-0.223	0.200	-1.281
TUA-L	16.5 (2-36)	-0.112	0.633	-0.478
OTU-H	16.9 (4-38)	-0.060	0.898	-0.128
OTU-M	14.5 (8-31)	**-0.321**	**0.058**	**-1.894**
TUA-H	31.7 (17-51)	-0.029	0.932	0.085
BOW-M	13.4 (4-32)	0.112	0.283	1.073
TMS-H	42.3 (22-55)	-0.191	0.293	-1.052
RNG-M	13.2 (4-57)	0.135	0.195	1.297
TAN-L	11.6 (5-19)	-0.026	0.916	0.105
TMS-L	3.8 (1-9)	-0.028	0.924	0.096
RNG-H	18.1 (3-39)	**0.206**	**0.094**	**1.677**
TMS-M	13.6 (4-32)	**0.256**	**0.034**	**2.117**
ONG-H	15.2 (4-24)	**-0.284**	**0.099**	**-1.651**
OMK-M	4.5 (1-9)	-0.070	0.845	-0.195
ONG-L	4.0 (1-24)	-0.079	0.802	-0.250
TP-H	19.7 (5-36)	-0.244	0.164	-1.392
OMK-H	10.7 (4-19)	-0.070	0.845	-0.195
TP-M	12.6 (9-31)	-0.126	0.547	-0.602
TP-L	8.6 (1-17)	-0.139	0.496	-0.681
OMK-L	6.0 (0-13)	0.133	0.238	1.180
ONG-M	7.6 (2-13)	-0.255	0.152	-1.434

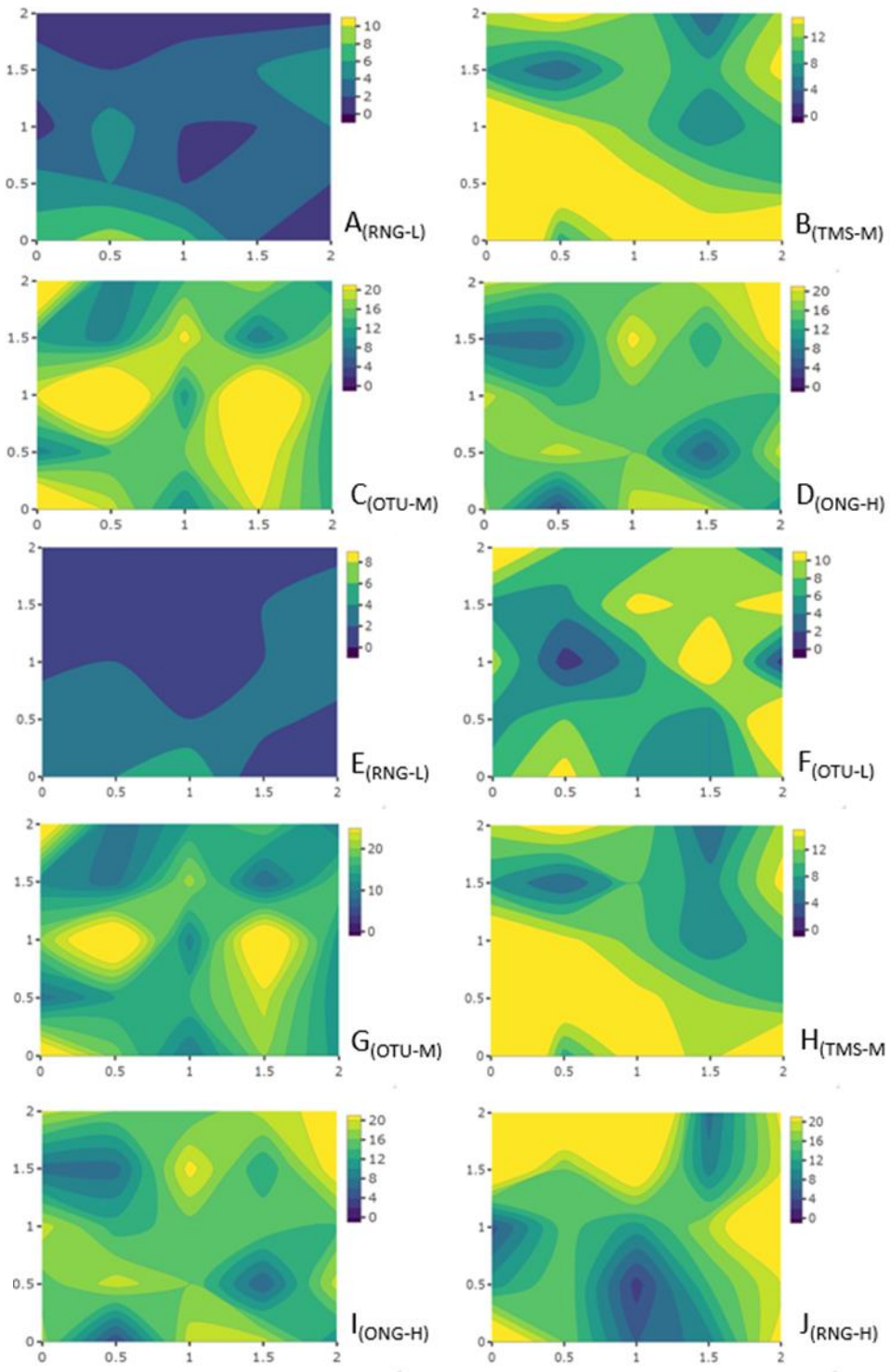

Figure 3.2: Contoured heatmaps of the 4 m^2 field survey plots that rejected the null hypothesis and have non-random patterning. A – D are plots that considered the total *Austrovenus* abundances. E – J are plots that considered only >10 mm ind. $core^{-1}$ *Austrovenus* abundances. Colour bar represents ind. $core^{-1}$ and colour represented vary between plots depending on the relative *Austrovenus* abundance of the plots.

3.2 Translocation experiment

3.2.1 Initial vs final translocated *Austrovenus* density

The majority of plots in the final *Austrovenus* abundance were less than the initial *Austrovenus* abundance which varied from -2 to -41 % loss (Table 3.5). There was a trend between the initial and final abundances where the average difference decreased with increasing *Austrovenus* abundance (Table 3.5). Low, medium and high-density plots had average differences of -1.7 %, -10 % and -18 % respectively. This trend may be a result of an increase in unaccounted individuals with increasing density. Although there was differing values of abundances between the final and initial *Austrovenus* abundances a distinct density gradient was still distinguished from low to high density plots (Table 3.5).

Table 3.5: Initial *Austrovenus* abundance (based off estimated density groups) vs Final *Austrovenus* abundance (based off six-week transplanted samples) from translocated plots.

Site	Initial *Austrovenus N* (ind. m^{-2})	Final *Austrovenus N* (ind. m^{-2})	Difference *Austrovenus N* (%)
LOW1	800	849	6
LOW2	800	474	-41
LOW3	800	1040	30
MED1	1600	1465	-8
MED2	1600	1631	2
MED3	1600	1219	-24
HIGH1	2500	1954	-22
HIGH2	2500	1754	-30
HIGH3	2500	2462	-2

3.2.2 Environmental variables

Med GS and mud % did not vary with *Austrovenus* density however OM content and pigments were affected (Table 3.6). As the translocated sites were situated in the same general area at Tuapiro Point (Appendix 2:A10) a distinct sedimentary gradient was not seen and the sediment composition of the sampled plots can be described as fine sand (185.5 ± 7.3 µm). Mud % ranged from 2.5 to 6.0 % and showed no evidence of differing with different density groups and ambient mud % e.g low-2, med-2 and high-3 had the highest mud % values being 5.9, 5.1 and 6.0 % respectively (Table 3.6). However, mud % did correlate with Med GS where there was a negative correlation of (R = -0.57; p = 0.052; Table 3.7).

OM content was low across all sampled plots with a range of 1.8 (AMB1) to 2.8 % (HIGH2). There was a high correlation between OM content and *Austrovenus* abundance (R = 0.73; p = 0.007; Table 3.7; Figure 3.3). Chl *a* content increased by almost a factor of two between the ambient and high plots from 11.3 µg g^{-1} dw (AMB1) and to 20.4 µg g^{-1} dw (HIGH3) (Table 3.6). Additionally, chl *a* correlated with OM content (R = 0.65; p = 0.021; Table 3.7). Similarly, to OM content, chl *a* also showed a strong correlation with mean *Austrovenus* abundance (R = 0.85; p = <0.001; Table 3.7; Figure 3.3). Phaeo content had a positive relationship with *Austrovenus* abundance (R = 0.58; p = 0.048; Table 3.7) and was strongly related to chl *a* content (R = 0.68; p = 0.015; Table 3.7). Average *Austrovenus* SL did not vary between the transplanted plots and there was an average of 21.5 (9.8-33.4) mm while the average *Austrovenus* SL in the ambient plots was slightly smaller 16.4 (10.1-23.3) mm (Table 3.6). The phaeo:chl *a* ratio did not differ between the transplanted plots and was strongly related to phaeo (R = 0.83; p = <0.001; Table 3.6 & 3.7), which was expected.

Table 3.6: Summary of *Austrovenus* and environmental variables from ambient and translocated plots. *Austrovenus N*: Mean *Austrovenus* abundance, *Austrovenus* SL: *Austrovenus* shell length, Med GS: median grain size, mud %: mud content, OM: organic matter, chl *a*: chlorophyll *a*, phaeo: phaeopigment. Bracketed values indicate the range.

Site	*Austrovenus* *N* (ind. core^{-1})	*Austrovenus* SL (mm)	Med GS (µm)	Mud (%)	OM content (%)	Chl *a* (µg g^{-1} dw)	Phaeo (µg g^{-1} dw)	Phaeo:Chl *a* ratio
AMB1	2.8 (0-6)	17.6 (9.6-22.8)	193	2.5	1.8	11.3	3.3	0.29
AMB2	2.1 (0-6)	14.6 (10.0-23.0)	183	4.4	1.8	14.0	4.8	0.34
AMB3	2.6 (0-6)	17.1 (10.6-24.2)	184	4.6	2.1	13.7	2.0	0.15
LOW1	5.5 (0-13)	20.5 (10.0-30.8)	183	3.6	1.9	13.4	5.8	0.43
LOW2	3.1 (0-10)	17.6 (11.2-28.6)	180	5.9	2.0	12.1	5.9	0.49
LOW3	6.8 (1-18)	21.2 (7.8-35.6)	190	4.0	1.8	12.7	3.8	0.30
MED1	9.5 (2-31)	22.7 (9.3-34.0)	186	2.8	2.2	13.7	3.3	0.24
MED2	10.6 (0-28)	22.4 (12.0-35.4)	190	5.1	2.5	14.8	4.8	0.32
MED3	7.9 (1-20)	21.5 (8.3-34.8)	176	3.9	2.2	16.4	4.0	0.24
HIGH1	12.7 (2-34)	22.8 (11.2-33.6)	189	3.2	2.4	19.5	8.7	0.45
HIGH2	11.4 (1-31)	22.7 (11.0-33.8)	199	3.5	2.8	18.2	4.8	0.26
HIGH3	16.0 (4-38)	21.7 (7.6-33.9)	173	6.0	2.3	20.4	7.5	0.37

Table 3.7: Pearson's correlation coefficient of environmental and biological variables of the translocated and ambient plots. Correlations with significant p-values (<0.05) shown in bold. Number of plots = 12.

	Med GS (µm)	Mud (%)	OM content (%)	Chl *a* (µg g^{-1} dw)	Phaeo (µg g^{-1} dw)	Phaeo:Chl *a* ratio
***Austrovenus N* (ind. core^{-1})**	-0.03	0.09	**0.73**	**0.85**	**0.58**	0.14
Med GS (µm)		**-0.57**	0.28	-0.24	-0.22	-0.16
Mud (%)			0.06	0.19	0.26	0.27
OM content (%)				**0.65**	0.29	-0.06
Chl *a* (µg g^{-1} dw)					**0.68**	0.17
Phaeo (µg g^{-1} dw)						**0.83**

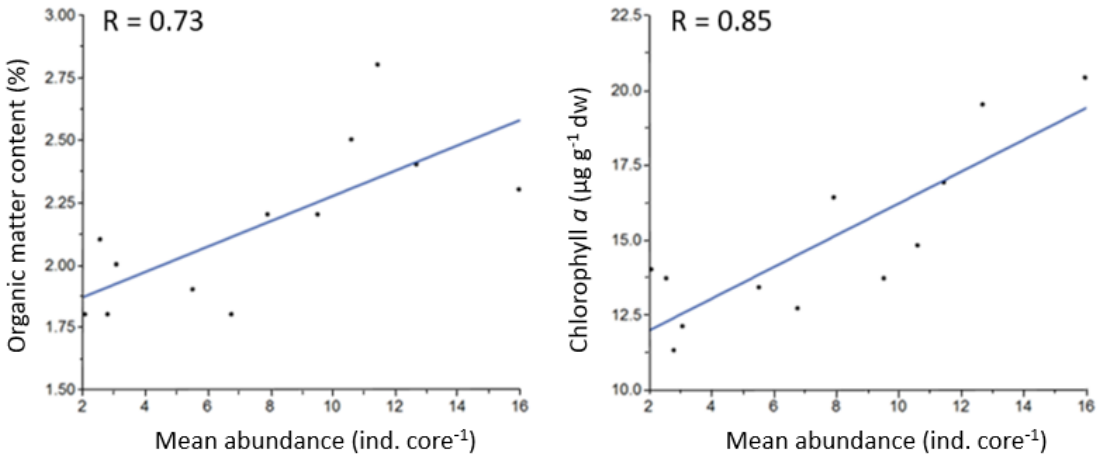

Figure 3.3: Linear correlation plots to visualise mean *Austrovenus* abundance (x) against multiple environmental variables (y) OM content (left) p = 0.007 and chlorophyll *a* (right) p = <0.001.

3.2.3 Ambient and translocation spatial patterns

From the translocation experiment there was a noticeable pattern in that increased *Austrovenus* abundance resulted in the likelihood of clustering behaviour to occur. Ambient *Austrovenus* abundance was generally < 8 ind. core^{-1} and displayed no distinct pattern as the null hypothesis was accepted and random contour patterns were in all three ambient plots (Table 3.8 & Figure 3.5). Of the low-density plots low-2 and 3 both had significantly positive Moran's *I* values which indicated moderate clustered patterns (Table 3.8). However, from inspecting the low-2 plot there is no indication of clustering of high values but rather negative clustering of low-density values which caused the rejection of the null hypothesis (Figure 3.5). Low-3 did experience clustering where a cluster of > 12 ind. core^{-1} in the centre of the plot is observed (Figure 3.5). Medium-1 was the only plot that showed signs of clustering across the plot with a significantly positive Moran's *I* value of 0.253 which indicated a moderate clustered pattern (Table 3.8). This is seen where a small cluster of >20 ind. core^{-1} occurs in the lower area of the plot (Figure 3.5). All three high density plots displayed significantly positive Moran's *I* values between 0.335 – 0.420 and from the high contour plots large clusters of >20 ind.

core^{-1} occur in the central area of each plot with low densities surrounding each cluster (Figure 3.5). The minimum density recorded that rejected the null hypothesis was 6.8 ind. core^{-1} (excluding the negative clustering of low-2) and the highest abundance was 16 ind. core^{-1} (Table 3.8). However, there was not a simple linear relationship between increasing *Austrovenus* and clustering as can be seen with medium-2 and 3 which accepted the null hypothesis. Additionally, high-3 had the greatest *Austrovenus* abundance but had a lower Moran's *I* value than high-1 and 2 which had lower abundances (Table 3.8). The abundance of *Austrovenus* in the extended 1 and 2 m samples from the outside of the plots showed minimal densities, comparable to the ambient density of the area which indicates *Austrovenus* individuals did not move outside of the plots border.

From the expected *Austrovenus* density plots it was predicted that for the low, medium and high plots that an abundance of 5, 10 and 16 ind. core^{-1} would be sampled respectively. This assumes complete uniformity on how the transplanted *Austrovenus* were laid out and no movement to take place. The cluster in low-3 was composed of values >12 ind. core^{-1} while the perimeter of the cluster was >5 ind. core^{-1} (Figure 3.5). The medium-1 cluster was small and consisted of values >20 ind. core^{-1}, samples surrounding the cluster were primarily >10 ind. core^{-1} (Figure 3.5). All three high density plots had clusters that were mainly composed of >20 ind. core^{-1} (Figure 3.5).

All replicates for the high-density treatment experienced clusters that were greater than the initial ind. core^{-1}, while the average *Austrovenus* abundance of the outer samples were synonymous of the three ambient plot *Austrovenus* abundances (Figure 3.4). This further affirms that the translocated site did not have a patchy distribution of

Austrovenus and suggests that *Austrovenus* would have had to move into these clusters to produce greater than expected abundance values.

Table 3.8: Global Moran's *I* statistics of the ambient and translocated *Austrovenus* plots ordered from lowest to highest Austrovenus abundance. Rejected null hypothesis shown in bold.

Site	***Austrovenus* N** (ind. core^{-1})	Moran's *I*	p-value	z-score
AMB2	2.1	0.132	0.239	1.177
AMB3	2.6	0.016	0.695	0.392
AMB1	2.8	0.105	0.326	0.982
LOW2	3.1	**0.259**	**0.029**	**2.186**
LOW1	5.5	0.115	0.285	1.070
LOW3	6.8	**0.295**	**0.023**	**2.276**
MED3	7.9	-0.009	0.823	0.224
MED1	9.5	**0.253**	**0.032**	**2.150**
MED2	10.6	0.168	0.146	1.452
HIGH2	11.4	**0.420**	**0.002**	**3.102**
HIGH1	12.7	**0.404**	**0.003**	**2.979**
HIGH3	16.0	**0.335**	**0.011**	**2.558**

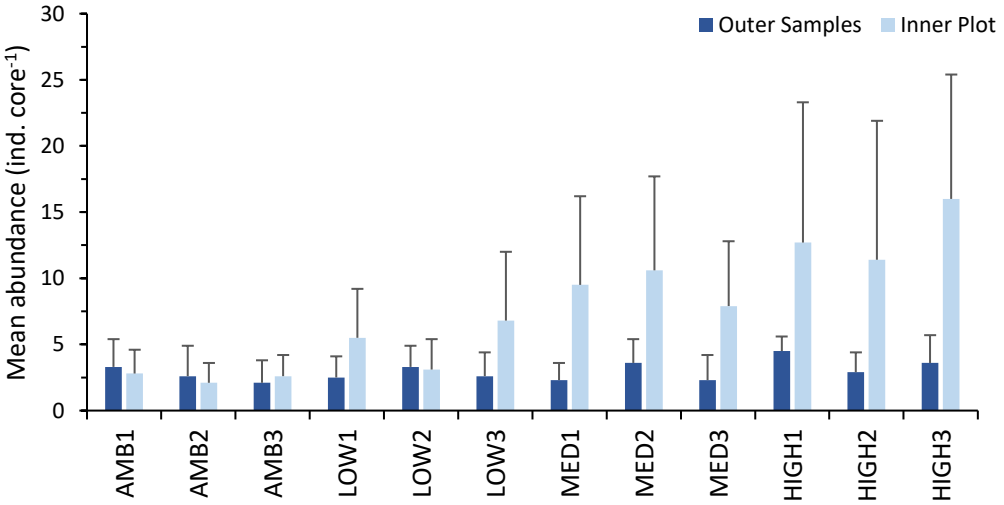

Figure 3.4: Mean *Austrovenus* abundance of the eight outer samples of each plot against mean *Austrovenus* abundance of inner plot with ± 1 SD of the mean *Austrovenus* abundance presented.

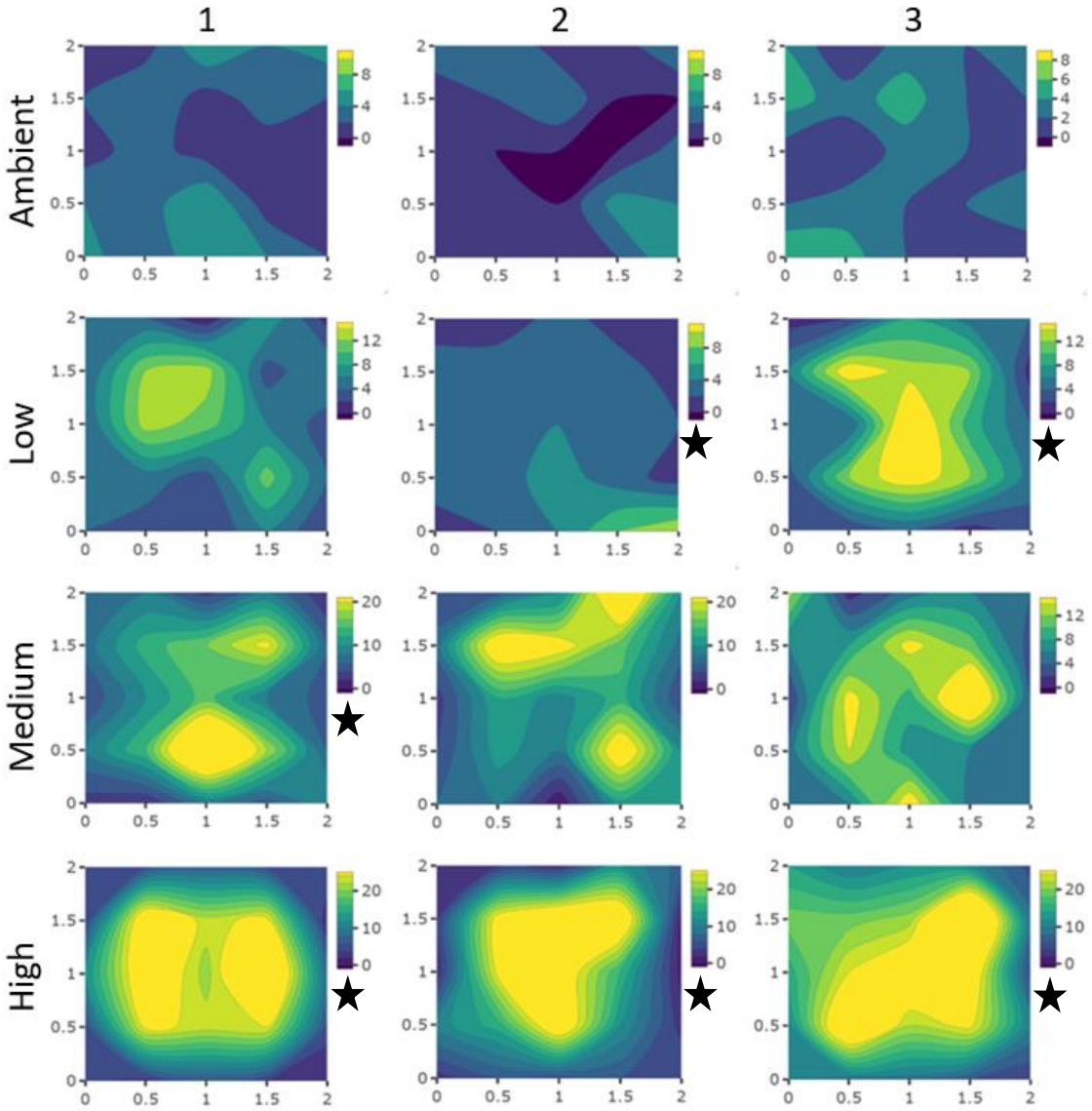

Figure 3.5: Contoured heatmaps of the 4m^2 translocated *Austrovenus* plots. From the top to bottom rows are ambient, low, medium and high *Austrovenus* density plots respectively and from left to right are replicates 1 – 3 respectively. Colour scale used to represent *Austrovenus* ind. core^{-1} and significant clusters indicated by a ★ symbol.

Chapter 4

Discussion

This study tested whether small-scale spatial patterns of *Austrovenus* are density dependent under natural conditions and whether translocated *Austrovenus* showed density dependent patterns of aggregation. Results showed that *Austrovenus* did not display any evidence of forming spatial patterns different from random within $4m^2$ plots of various density beds or with differing environmental variables as observed from field based surveys. However, within the translocation experiment observations of spatially clustered patterns in $4m^2$ plots were shown to be persistent in plots with higher densities of *Austrovenus*. Additional observations of the translocation experiment showed that there was also an increase of both chlorophyll *a* (chl *a*) and organic matter (OM) content with increasing *Austrovenus* plot densities.

4.1 Field survey

4.1.1 Field survey spatial patterns

There was no evidence of spatial structuring dependent on density or mud content, where the majority of *Austrovenus* plots were randomly distributed. This was confirmed where 21 out of 27 plots failed to reject the null hypothesis when juveniles were excluded. Of the six plots that did reject the null hypothesis, half were dispersed, and half were clustered, likely a result of type-1 error. Observing similar distribution patterns of *Austrovenus* across the majority of plots increases confidence that the random patterns were not a result of abiotic stressors of the local environment e.g. differing wave exposure and mud content and also not a result of a density gradient but rather

the biotic processes that can be attributed to the various sites e.g. active movement, individual interactions, recruitment and/or predator pressures.

Previous studies have provided mixed evidence of spatial patterns of infaunal suspension feeding bivalves, explaining how random or clustered patterns are observed. The results are likely due to the fact that various studies have investigated spatial patterns at differing spatial scales. At large scales of tens of metres – kilometres spatial patterns of bivalves are often related to environmental conditions (such as mud content) (Chapman, 2000; Legendre *et al*., 1997; Ysebaert & Herman, 2002). These large-scale studies have found that dominant infaunal suspension feeding bivalves tend to form large clustered patterns. A study by Boldina & Beninger (2013) for example found that mean densities of *Cerestoderma edule* showed clustering patterns in all plots that could assess spatial distribution. Patches of clustering were documented at a distance of <300 m but more so between 0 and 60 m. Additionally, Huxham & Richards (2003) recorded spatial aggregation of *C.edule,* with a patch having a spatial range of 20 m^2. Kraan *et al*. (2009) demonstrated that *C.edule* can form patches with a spatial range of up to 2000 m. These three studies therefore document differing spatial scales at which clustering was observed for *C.edule* likely related to the scale that the research was focused on. Processes operating at smaller scales within intertidal benthic ecology are currently not as well researched (Ellis & Schneider, 2008) and at smaller scales behavioural interactions and feedback of bivalves are more likely to explain spatial patterns (Thrush, 1991; Hewitt *et al*., 1996). This study therefore investigated aggregation patterns across small scales addressing a research gap.

The sampling scale of 4 m^2 used in this study was suited to distinguish small scale feedbacks influenced by behaviours as opposed to large scale patches. Hewitt *et al*.

(1996), used 6 m as the upper scale of their sampling design and recommended a scale of < 5 m as this scale would be where individual crawling movement and inter-individual interactions were conceived to be influential. Similar to the present study Richardson *et al.* (1993) found that *C.edule* was distributed randomly at a maximum scale of 1 m^2. Although Richardson *et al*. (1993) found random spatial patterns similar to observations of this field survey, only one three plot replicates were sampled in the same intertidal location, all with low *C.edule* densities. Contrary, Hewitt *et al*. (1996) found that adult *Austrovenus* demonstrated spatial structuring at small scales in both a sandy and muddy site where clustering was shown to form at a 1.3 m diameter patch nested within a 3 – 3.7 m diameter patch. This may be due to Hewitt *et al*. (1996) using a finer spatial lag of sampling than this study which increased the precision of the spatial patterns observed, nevertheless Hewitt's study lacked site replication.

Overall random spatial patterns were observed in this study for both adults and juveniles in the natural environment. A number of factors could be involved in the random patterns observed. Epibenthic predation history of the patch which can include predators such as fishes, humans, rays, shorebirds, starfishes, and crustaceans (Thrush, 1999) can remove clustering patterns in shellfish. For example, the impact of horseshoe crabs, *L. polyphemus*, on the clam, *Gemma gemma,* was assessed through a predator exclosure experiment. *G. gemma* were aggregated when protected from *L. polyphemus* and distributions were more random in unprotected plots (Botton, 1984). Homogenization or the neglect of organized spatial patterns of the spatial distribution can be explained by Lèvy type foraging strategy which can be adopted by most predators. For example, oystercatchers can determine patches of highest *Austrovenus* density and will prioritize feeding in these patches (Sutherland, 1982; Thomas *et al*., 2020). A translocation experiment performed by Whitlach *et al*. (1997) found a greater

proportion of nipped siphons (11 – 37 %) in *Austrovenus* of large patches (9 m^2) compared to smaller patches (0.25 m^2). Elliott *et al.* (2009) also described that predators that forage with random movement in the absence of visible patches but would manoeuvre directly to detectable patches are likely to follow a Lèvy search pattern. This could explain the small-scale random distribution of *Austrovenus* in the natural environment where predators have removed the aggregated patterns by feeding on clusters and *Austrovenus* have dispersed themselves randomly to reduce the detectability of clusters and reduce mortality as a result of the increased effort for predators required to feed on individuals. These random patterns may then be nested within broader patchiness that is evidenced across larger scale environmental gradients, which as mentioned above, are widely observed.

4.1.2 Field survey environmental variables

The relationship between *Austrovenus* abundance and shell length (SL) with environmental variables were not linearly related. The sampling design required selection of sites where *Austrovenus* was abundant within a homogeneous substrate which allowed for sampling of low/medium/high relative densities and across multiple variations of environmental variables. No observed relationships between density and environmental variables e.g. mud content across this relatively restricted gradient were observed because a relatively narrow range of conditions were considered. Since this was not a study focusing on the environmental gradient, examples of linearity from the literature that specifically looked at environmental gradient effects were not expected to be observed. For example, *Austrovenus* abundance has shown to be negatively linearly correlated with increasing mud content (e.g. Pratt *et al*. (2014) and Thrush *et al*. (2003)). *Austrovenus* SL was expected to increase with greater exposure. This is because

larger *Austrovenus* are associated with high energy environments whereas smaller individuals particularly juveniles are susceptible to being uplifted and transported. For example, Norkko *et al*. (2001) found that juveniles were uplifted and dispersed over scales of metres during a single tidal cycle. Another factor is that high muddier environments have high suspension sediment loads, reducing feeding efficiency and loss of utilisable energy sources such as protein and sugars, adversely affecting reproduction and growth (Ellis *et al*., 2002). OM content was negatively related to median grain size (Med GS) and positively correlated to mud content, this linearity has previously been recorded in earlier studies (Flemming & Delafontaine, 2000; Keil & Hedges, 1993; Lee *et al*., 2019). This is due to muddy sediment having greater adsorption capacity than sandy fractions, a result of having a larger surface area (Keil & Hedges, 1993; Burdige, 2007) and are generally low energy environments, so resuspension of fine particles bound with OM content is low.

Species-environment relationships are often asymmetric, nonlinear and show heterogeneous scatter. These data points are generally scattered between an upper and lower limit, previously described as a 'factor ceiling' (Thomson *et al*., 1996). Furthermore, variances are smaller in areas of the scatter where mean abundance values are small, in which environmental conditions can be sub-optimal. The ceiling of the scatter suggests a constraining factor, the form of the ceiling can then allow a maximum response curve to be derived for a target environmental variable e.g. mud content (Thrush *et* al., 2003). This implies that, across many scales, although multiple factors can affect observed densities (e.g. recruitment processes, competition/predation) there is a limit (in this case an upper limit) which the variable in question controls. By modelling the upper quantile rather than the mean not only is heterogeneity considered, but also associates the ecological concept that confounding variables pose as limitations against organisms

(Cade *et al*., 1999, 2005; Lancaster & Belyea, 2006). Peaks within the model indicate an estimated optimum for species, in this case *Austrovenus*.

Maximum abundance models of the response of *Austrovenus* to environmental stressors were generated. *Austrovenus* abundance was adversely affected by increasing mud content. Where low mud content was beneficial while increased mud content resulted in the decrease of *Austrovenus* abundance. This unimodal response and optimum upper limit of *Austrovenus* against mud content is comparable to previous estimates of 9.2 – 11.3 % from various studies e.g. (Anderson, 2008; Ellis *et al*., 2017; Norkko *et al*., 2002; Thrush *et al*., 2003). Elevated suspended mud particles can result in reduced feeding efficiency (e.g. reduced nutritional value of seston and clogging of feeding apparatus) and ultimately a decline in the abundance of *Austrovenus* (Cheung & Shin, 2005; Ellis *et al.*, 2004; Norkko *et al.*, 2006; Thrush *et al*., 2003; Turner & Miller, 1991). Wave exposure also had a unimodal response to the maximum *Austrovenus* abundance, this is likely due to smaller individuals being more susceptible to being uplifted in high energy environments than larger individuals, thus reducing overall density. However, low wave exposure experience low abundances as these areas are generally areas with higher mud content which mentioned above reduce the feeding capabilities of *Austrovenus* inhibiting reproduction and growth due to lack of utilizable nutrients (Ellis *et al*., 2002). Both OM and chl *a* shared almost identical unimodal response surfaces, likely due to the strong linkage between OM and MPB biomass. As OM is reminiralized inorganic nutrients are regenerated and supplement the growth of MPB (Lohrer *et al*., 2004). However there appears to be a critical point where a density-dependent negative feedback occurs to which the elevated bioturbation activity may result in OM, chl *a* and phaeopigment (phaeo) to resuspend thus only a lesser percentage of OM and pigments remain on the sediment surface. Similarly, Ciutat *et al*.

(2007) found that sediment resuspension was elevated with increasing density treatments of *C. edule*, where suspended sediment concentrations went from 574 to 2253 mg L^{-1} for 47 and 312 ind. m^{-2}, directly related to the increase of bed roughness and bioturbation.

4.2 Translocation experiment

4.2.1 Translocation spatial patterns

Converse to the field survey, *Austrovenus* showed clustering behaviour with increasing patch density at the same sampling scale as the field survey. High density plots showed statistically significant clustering and is likely a result of having the high density treatments not being associated within a larger beds (no conspecific interactions beyond plot boundary) and that various mechanisms in the experiment could have provided an optimal environment for *Austrovenus* including, lack of predation, low mud content and low wave exposure. The low density plots may not have experienced clustering as the densities were low, which allowed individuals to spread out and is likely that individual encounters were low so behaviour did not lead to clustering. This was particularly recognized in the low replicate with a 41 % decrease in the observed abundance, which was most likely caused by human error during the transplanting process. Although, one low density replicate was 30 % more abundant than the expected *Austrovenus* abundance, this could potentially be the reason why a small cluster occurred, unlike the other low replicates which had a random distribution. For two of the three medium density plots structuring was more evident than in the low plots, possibly due to the increased density. Similarly, Liu *et al*. (2013) and van de Koppel *et al*. (2008) found that lower densities of the blue mussel, *Mytilus edulis*, tended to lack apparent structure and were patchy which lacked the “labyrinth-like” pattern that was seen in higher densities.

Mechanisms that may influence the observed density dependent aggregation patterns in this study include predation and movement of bivalves out of high areas due to competition. Although there was visible mortality of *Austrovenus* observed there was no clear evidence of predation e.g. shore birds or ray pits. Most likely as a result of selecting a site not commonly abundant of *Austrovenus* which predators would naturally avoid while the plots were also small enough for predators to not detect. *Austrovenus* may not have moved outside of the designated plots as there would be no adaptive benefit in doing so as it is evident there is more food available within the plots which is especially so with the high MPB biomass of the higher density plots. Additionally, the temporal scale of six weeks was sufficient, given *Austrovenus* can move 30 cm per tidal cycle as they burrow through surface sediment (Mouritsen, 2004). Furthermore, in a past translocation study van de Koppel (2008) found that the evolution of non-structured to labyrinth-like structures in lab-controlled *M. edulis* happened very rapidly (within 24 h), although both species differ in their movement speed the self-organizing behaviour can be noted for both species. Therefore, this clustering behaviour can be considered a long-term behaviour as there was no beneficial outcome towards survival for *Austrovenus* to move beyond the plot boundary, which the species have proven to be capable of doing so (Mouritsen, 2004). The clustering response may also be an attempt by *Austrovenus* to reduce dislodgement by wave activity further supporting the concept of their resilience in space over time, similar to that of *M. edulis*. A study by Bertolini *et al*. (2019) found that homogeneous and striped patterns of *M. edulis* where most resistant to water flow in a controlled flume experiment where nearly no movement or dislodgement occurred, compared to small clusters and 'sparse' patterns which showed higher dislodgment rates. Furthermore, bed shear stress and bioturbation activity increase vertical mixing allowing the bivalves to resuspend MPB,

providing the bed with an important food source (Jones *et al*., 2011b). Which may also contribute to the clustering observed in the high-density plots.

This concept of *Austrovenus* remaining within the plot boundaries can plausibly explain the random patterning behaviour seen within the plots of the field survey. What was lacking from the translocation experiment was that the plots were not present within an abundant *Austrovenus* bed and would not experience the individual interactions of conspecifics beyond the translocation plot boundary. Naturally occurring beds are frequently extensive and from a given point it is likely for an individual *Austrovenus* to interact with another thus the range of conspecifics is large and clustering behaviour would not be required, highlighting the density dependency of ambient *Austrovenus* abundance for random spatial patterns to occur.

4.2.2 Effects of translocated plots

Higher densities of transplanted *Austrovenus* resulted in an increase of OM and chl *a* within plots while lower densities did not result in elevated OM and chl *a* relative to ambient plots. This is likely due to a positive feedback of greater output of nutrients excreted as urine stimulating MPB. This is supported by earlier studies where *Austrovenus* and other bioturbating macrofauna have found an increase in MPB productivity with increasing biomass, even though MPB is majorly grazed upon by these animals (Sandwell *et al*., 2009; Thrush *et al.*, 2006; Woodin *et al*., 2016). This is unlikely to be a result of grazing and faecal deposits as the ratio of chl *a* to phaeo was fairly low ranging from 15 – 49 % of phaeo to chl *a* and did not vary between the ambient and treatment densities. This indicates that there is a positive feedback where *Austrovenus* are stimulating primary production in-situ through excretions and due to the high density and clustering formation of adult *Austrovenus*. Woodin *et al*. (2016) and

Sandwell *et al*. (2009) both found that increases in primary productivity in response to increased *Austrovenus* density which was directly linked to ammonium excretion of *Austrovenus* rather than activity. However, Woodin *et al*. (2016) found that the mechanism for increased primary production for species that differ in feeding mode (bioirrigation) and movement (bioturbation) as a result of a larger substrate surface area being formed allowing for greater primary production potential. If the increase of chl *a* was from faecal sources, then the phaeo:chl *a* ratio would be expected to be greater with increasing abundance treatment, as phaeo is an indicator of refractory/degraded pigment biomass (Pratt *et al*., 2014). Also, the sediment conditions of the translocation site was well suited for facilitating MPB (173-199 µm Med GS & 2.5-6.0 % mud). Jones *et al*. (2011a) found that the ability for *Austrovenus* to facilitate MPB productivity is greater in sandy than muddy sediment, due to muddy sediment having lower permeability, lower light, reduced oxygen penetration depth and rates of nutrient transport. The slight increase of OM content with increasing density is most likely due to a positive feedback of there being more individuals excreting faecal deposits contributing to chl *a* content and although not at the scale of excreted ammonium, primary production would also be supported.

Whilst patterns in the OM and chl *a* were observed with density, grain size properties did not differ. Both Med GS and mud content were not altered by the differing density treatments of *Austrovenus* having similar properties to the ambient sediments. Grain size was not expected to differ between each plot as a sediment gradient was not targeted (plots in close proximity; affected by same abiotic stress). Additionally, although sediment resuspension is elevated with increasing density (Ciutat *et al*., 2007) the effect on resuspension is likely to not be that great because the translocated site is a low energy environment (e.g. sheltered shore with an absence of wave ripples). These

findings confer with results from Sandwell et al. (2009) where med GS and mud were not correlated with differing translocated *Austrovenus* densities and Thrush (2006) who found that the removal of *Austrovenus* did not affect sediment grain properties over an 8-week period, although the study lacked density treatment effects.

4.3 Limitations

The results of this study should be considered in light of some limitations. There is a possibility that the spatial lag of 0.5 m between each core sample, although logistically allowed sampling of three plots within one tidal cycle, may not have been fine enough to identify small-scale spatial patterns, resulting in random spatial distributions. The study was also time limited where the predation history of each field survey was not evaluated prior to sampling. This could have been a potentially important confounding factor to help explain *Austrovenus* distributions. Low juvenile numbers could have been the result of the sampling method. Normally a smaller meshed sieve e.g. 500 µm would be used to obtain juveniles and since sampling was constrained by tidal regimes, time spent removing juveniles from the sieves was limited. The lack of juveniles can also be attributed to sampling late in the spawning season where juveniles were less abundant. This potentially caused the juvenile abundances for this study to be underreported.

Limitations also occurred in the translocation experiment. The experiment lacked extensive replication with only three low, medium and high plots being produced. With more replicates a conclusion of the effects of the different density treatment beds on environmental variables and spatial patterns could be made with greater confidence. The study was also limited to one location so environmental heterogeneity was not considered. It would be beneficial to have multiple site replicates varying across differing environmental conditions to observe any variations of spatial patterns and chl *a* content.

4.4 Study implications

This study has wider implications towards enriching the knowledge of benthic ecology, not limited to *Austrovenus* but specifically towards spatial patterns of intertidal infaunal suspension bivalves. This study is to our knowledge the first of its kind to observe small-scale spatial patterns of infaunal bivalves across various intertidal locations and within translocated beds (which has only previously been done in a lab environment). Research on small-scale patterns of infaunal bivalves is currently lacking and therefore this research addresses this current gap. There is also potential for these high-density translocated plots to act as nursery grounds for reseeded juvenile *Austrovenus* due to the modified environment becoming nutrient rich. It would be interesting to see if juvenile *Austrovenus* grow faster within higher density clustered plots as a result of the positive feedback of greater food availability and a more stabilized habitat. This would have further implications for conservation and restoration of the species where recovered environments could have these plots manually reintroduced which would eventually help restore ecosystem functioning.

4.5 Future research

Modifications of the field experiment could be performed to improve the knowledge presented from this study's results. By increasing the spatial lag of samples within plots there would be greater confidence in the resulting spatial patterns of the field survey, due to an increase in precision. Another factor to consider in future research is to understand the predation history of the area that plots are sampled from through preliminary surveys on predator or predation structures e.g. ray pits. This would help in concluding how important predation is towards forming observed spatial patterns. A modification of the translocation experiment could be that translocated plots of the

same scale as this study could be transplanted into well-distributed *Austrovenus* beds. Observations can then be made on the movement of *Austrovenus* whether clustering occurs again at high transplanted densities or if *Austrovenus* now move beyond the plot boundary which would support the notion that there is an ambient density dependence for *Austrovenus* to form random distributions or not.

4.6 Conclusion

Spatial autocorrelation of low, medium and high-density plots and associated environmental variables were measured in nine well-distributed *Austrovenus* beds as well as a translocated site in Tauranga Harbour. This study provided insight on the spatial patterns of *Austrovenus* and how density dependent spatial structures have important ecosystem functioning capabilities. Overall, the key findings from this study were:

- *Austrovenus* did not exhibit spatial patterns relative to random distributions in natural beds and was not dependent on density.
- *Austrovenus* did not exhibit spatial patterns different to random in natural beds depending on environmental variables.
- Transplanted *Austrovenus* beds exhibited clustering in high density treatments with clustering being more prominent in high density treatments.
- Transplanted *Austrovenus* beds in low density treatments had random patterns.
- Transplanted *Austrovenus* beds significantly improved sediment chl *a* content with increasing density treatments. However, only a small increase in OM content was observed and no modifications were seen in sediment grain properties.

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Appendices

Appendix 1. GPS Coordinates of Sampled Plots

Table A1. The GPS coordinates of sites within the Tauranga Harbour (NZGD2000)

Site	Latitude	Longitude
BOW-L	37°27'25.71"S	175°58'25.45"E
BOW-M	37°27'26.18"S	175°58'25.11"E
BOW-H	37°27'26.49"S	175°58'24.95"E
OMK-L	37°38'26.19"S	176° 2'48.33"E
OMK-M	37°38'28.51"S	176° 2'50.98"E
OMK-H	37°38'27.22"S	176° 2'50.13"E
ONG-L	37°30'8.37"S	175°58'13.62"E
ONG-M	37°30'11.09"S	175°58'22.49"E
ONG-H	37°30'7.90"S	175°58'21.93"E
OTU-L	37°39'57.46"S	176° 9'24.67"E
OTU-M	37°39'54.51"S	176° 9'21.86"E
OTU-H	37°39'55.69"S	176° 9'25.82"E
RNG-L	37°42'19.87"S	176°11'29.01"E
RNG-M	37°42'20.25"S	176°11'30.59"E
RNG-H	37°42'21.39"S	176°11'28.19"E
TAN-L	37°28'58.22"S	175°57'8.08"E
TAN-M	37°28'59.44"S	175°57'10.84"E
TAN-H	37°28'58.11"S	175°57'12.62"E
TP-L	37°39'43.25"S	176° 2'40.20"E
TP-M	37°39'43.94"S	176° 2'41.52"E
TP-H	37°39'46.63"S	176° 2'43.24"E
TUA-L	37°29'14.23"S	175°57'23.44"E
TUA-M	37°29'13.24"S	175°57'23.21"E
TUA-H	37°29'14.44"S	175°57'22.01"E
TUA(SM)-L	37°29'24.10"S	175°56'41.66"E
TUA(SM)-M	37°29'24.40"S	175°56'43.30"E
TUA(SM)-H	37°29'13.89"S	175°56'45.03"E

Table A2. GPS coordinates of translocated *A. stutchburyi* plots at Tuapiro Point, New Zealand (NZGD2000).

Site	Latitude	Longitude
AMB1	37°29'23.66"S	175°57'0.24"E
AMB2	37°29'23.65"S	175°57'0.37"E
AMB3	37°29'23.61"S	175°57'0.32"E
LOW1	37°29'23.73"S	175°57'0.28"E
LOW2	37°29'23.74"S	175°57'0.33"E
LOW3	37°29'23.63"S	175°57'0.36"E
MED1	37°29'23.71"S	175°57'0.23"E
MED2	37°29'23.69"S	175°57'0.33"E
MED3	37°29'23.64"S	175°57'0.24"E
HIGH1	37°29'23.67"S	175°57'0.28"E
HIGH2	37°29'23.69"S	175°57'0.37"E
HIGH3	37°29'23.64"S	175°57'0.28"E

Appendix 2. Location of Sampling Plots

Figure A1. Location of Bowentown sampling plots.

Figure A2. Location of Omokoroa sampling plots.

Figure A3. Location of Ongare sampling plots.

Figure A4. Location of Otumoetai sampling plots.

Figure A5. Location of Rangataua sampling plots.

Figure A6. Location of Tanner's Point sampling plots.

Figure A7. Location of Te Puna sampling plots.

Figure A8. Location of Tuapiro Point sampling plots.

Figure A9. Location of Tuapiro (muddy-sand) sampling plots.

Figure A10. Distribution of translocated sampling plots at Tuapiro Point (A = Ambient, L = Low, M = Medium and H = High).